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Full Name of Author — Nom complet de l'auteur: SUMMERS, PETER SCOTT

Date of Birth — Date de naissance: 21-6-56

Country of Birth — Lieu de naissance: CANADA

Permanent Address — Résidence fixe: RR#3, GUELPH, ONTARIO, N1H 6H9

Title of Thesis — Titre de la thèse: Translocation Studies of Glyphosate and Picloram in Canada Thistle [Cirsium arvense (L.) Scop.]

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Name of Supervisor — Nom du directeur de thèse: W. H. Vanden Born

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Translocation Studies of Glyphosate and Picloram in Canada Thistle [*Cirsium arvense* (L.) Scop.]

by

©

Peter S. Summers

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **Translocation Studies of Glyphosate and Picloram in Canada Thistle [*Cirsium arvense* (L.) Scop.]** submitted by Peter S. Summers in partial fulfilment of the requirements for the degree of Master of Science in Weed Science.

....

Supervisor

John Hoddinott

Saul Zalik

Date Aug. 27, 1981

Abstract

The translocation of glyphosate and picloram in Canada thistle was investigated using two plant systems, one being a 6-week old plant trimmed to possess only a green basal leaf and an apex, and the second was a 1-week old shoot with 20 cm of attached root.

The absorption of picloram by the young leaves of the apex was greater than by the mature basal leaves. No difference in absorption of glyphosate by the apical or basal leaves was noted. Of the ^{14}C-glyphosate applied to a basal leaf of the first plant system, 15 and 4% was later recovered in the apex and stem, respectively. The corresponding amounts for ^{14}C-picloram were significantly lower at 2 and 1.5%. After application to the apex of the same plant system, only glyphosate was translocated basipetally in significant amounts. Girdling the stem below a basal leaf did not significantly alter the subsequent distribution pattern of ^{14}C-picloram after basal or apical leaf application. Of the herbicide applied inside a lanolin ring on the basal leaf, 4.7 and 1.6% of the picloram and glyphosate, respectively, was retained by the lanolin.

In the second plant system the translocation of picloram from a treated young shoot to the roots was negligible. On the other hand, 4.5% of the ^{14}C-glyphosate applied to the young shoot had moved basipetally out of the shoot into the lower stem and root sections. The amount of ^{14}C-glyphosate in the root had peaked 74 hours after treatment at approximately 15000 dpm (3.4% of the dose applied).

In a field experiment, ethephon applied 2 weeks prior to a treatment of glyphosate increased the control of Canada thistle, compared to treatments consisting of glyphosate alone, tank-mixes of glyphosate and ethephon and similar combinations of ethephon and dicamba.

Glyphosate was more mobile than picloram in the two Canada thistle plant systems used in this study. It appeared that glyphosate was able to reach plant tissue, such as the roots of a young shoot, when no apparent major sink for assimilates was present. The significance of this observation to weed control in the field and further research is discussed.

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Table of Contents

Chapter Page

1. INTRODUCTION 1

2. LITERATURE REVIEW 4

    2.1 Biology of Canada Thistle 4

    2.2 Perennial Weed Control 5

    2.3 Translocation of exogenous and endogenous substances in plants 9

    2.4 Picloram 16

    2.5 Glyphosate 21

3. MATERIALS AND METHODS 28

    3.1 Plant Material 28

        3.1.1 Whole Plant Studies 28

        3.1.2 Shoot-Root Studies 29

    3.2 Radioactive Chemicals 29

    3.3 Treatment of Plant Material 32

        3.3.1 Whole Plant Studies 32

            3.3.1.1 The Absorption and Translocation of ^{14}C-glyphosate and ^{14}C-picloram from Basal and Apical Leaves .33

            3.3.1.2 Basipetal Transport from the Apex 34

            3.3.1.3 The Translocation of ^{14}C-assimilates from a Basal Leaf Exposed to $^{14}CO_2$ 34

            3.3.1.4 The Effect of Girdling on Acropetal and Basipetal Translocation .34

            3.3.1.5 Translocation of Non-radioactive Chemicals Past a Petiole Girdle ..35

        3.3.2 Shoot-root Studies 36

            3.3.2.1 Shoot-root Mutilation Studies Involving a Series of Doses of Glyphosate and Picloram 36

        3.3.2.2 Translocation of Shoot-applied ^{14}C-glyphosate and ^{14}C-picloram into the Root Tissue 37
        3.3.2.3 Effect of Shoot Size on Herbicide Translocation into Root Tissue 37
    3.3.3 Retention of Herbicides by Lanolin Rings 38
  3.4 Determination of Radioactivity in Plant Tissues 38
    3.4.1 ^{14}C-glyphosate 38
    3.4.2 ^{14}C-picloram 40
    3.4.3 ^{14}C-assimilates 42
  3.5 Liquid Scintillation Spectrometry 42
  3.6 Field Experiment 44
  3.7 Statisical Analysis 46
4. RESULTS AND DISCUSSION 47
  4.1 The Absorption and Translocation of ^{14}C-glyphosate and ^{14}C-picloram from Basal and Apical Leaves 47
  4.2 Basipetal Transport from the Apex 60
  4.3 The Translocation of ^{14}C-assimilates from a Basal Leaf Exposed to $^{14}CO_2$ 62
  4.4 The Effect of Girdling on Acropetal and Basipetal Translocation 63
  4.5 Translocation of Non-radioactive Herbicides Past a Petiole Girdle 65
  4.6 Shoot-root Mutilation Studies Involving a Series of Doses of Glyphosate and Picloram 68
  4.7 Translocation of Shoot-applied Herbicide into Root Tissue 69
  4.8 Effect of Shoot Size on Herbicide Translocation into Root Tissue 76
  4.9 Retention of Herbicide by Lanolin Rings 79
  4.10 Ethephon Treatments in the Field 81
  4.11 General Discussion 84

BIBLIOGRAPHY 88

APPENDIX : Analysis of Variance Tables 103

List of Tables

Table Page

I. Regression lines applied to liquid scintillation count data in order to correct for quenching in four combinations of fluor and solvent. 45

II. Total radioactivity (as % of applied dose) recovered from source-sink plant systems following ^{14}C-picloram or ^{14}C-glyphosate treatment to the apical or basal leaf. Expt. 3.3.1.1 48

III. Recovery of ^{14}C-activity from stems and basal leaves following ^{14}C-herbicide treatment of the apical leaves. Expt. 3.3.1.2 61

IV. Distribution of ^{14}C-activity in Canada thistle following exposure of a mature leaf to $^{14}CO_2$ (x1000 dpm). Expt. 3.3.1.3 63

V. The effect of steam-girdling the stem below a basal leaf on the recovery of ^{14}C-activity from source-sink plant systems 3 days following ^{14}C-picloram treatment of the apical leaves. Expt. 3.3.1.4 64

VI. The effect of steam-girdling the stem below a basal leaf on the recovery of ^{14}C-activity from source-sink plant systems 3 days following ^{14}C-picloram treatment of the basal leaf. Expt. 3.3.1.4 64

VII. Fresh and dry weights of plant apices, 22 days after herbicide and girdling treatments to the basal leaf. Expt. 3.3.1.5 66

VIII. The effect of time required for translocation and herbicide dose on the translocation of a lethal amount of picloram or glyphosate from the shoot to the roots of a shoot-root system. Expt. 3.3.2.1 69

IX. The total amount of ^{14}C-activity recovered from the root sections and lower stem of a shoot-root system after ^{14}C-picloram treatment of the shoot. Expt. 3.3.2.1 70

X. Regression lines for the recovery of ^{14}C-glyphosate between hours 2 and 74 from various sections of a shoot-root system following treatment of the shoot. Expt. 3.3.2.2 76

XI. Reported partition coefficients (1-octanol/water) and water solubilities for herbicides. 80

XII. Control of Canada thistle by treatments of ethephon with dicamba or glyphosate in the field. Expt. 3.6. 82

List of Figures

Figure Page

1. Canada thistle source-sink plant system used in Experiments 3.3.1 30

2. Canada thistle shoot-root plant system used in Experiments 3.3.2 30

3. Percentage reduction in liquid scintillation counting efficiency due to chlorophyll quenching. ...43

4. Percentage reduction in liquid scintillation counting efficiency due to quenching from water-extracted Canada thistle root pigments. 43

5. Recovery of ^{14}C-activity from leaf washes following apical and basal leaf ^{14}C-herbicide treatments. Expt. 3.3.1.1 51

6. Recovery of ^{14}C-activity from ^{14}C-herbicide treated apical leaves. Expt. 3.3.1.1 52

7. Recovery of ^{14}C-activity from ^{14}C-herbicide treated basal leaves. Expt. 3.3.1.1 52

8. Recovery of ^{14}C-activity from stems following ^{14}C-herbicide treatments to a basal leaf. Expt. 3.3.1.1. 56

9. Recovery of ^{14}C-activity from apices following ^{14}C-herbicide treatments to a basal leaf. Expt. 3.3.1.1. 57

10. Dpm/gram of fresh apical leaves following a ^{14}C-herbicide treatment of the basal leaf. Expt. 3.3.1.1. 59

11. Recovery of ^{14}C-activity from the stem intervening a ^{14}C-herbicide treated apex and a basal leaf. Expt. 3.3.1.1. 61

12. The appearance of new leaves in the apex following herbicide and girdling treatments to the basal leaf. Expt. 3.3.1.5. 67

13. Recovery of ^{14}C-activity, over time, that has been translocated to the root sections and lower stem following treatment of the shoot with ^{14}C-glyphosate. Expt. 3.3.2.2. 72

14. Recovery of ^{14}C-activity from the lower stem, over time, following treatment of the shoot with ^{14}C-glyphosate. Expt. 3.3.2.2. 73

15. Recovery of ^{14}C-activity from the root sections, over time, following treatment of the shoot with ^{14}C-glyphosate. Expt. 3.3.2.2. 74

16. Recovery of ^{14}C-activity translocated to the root sections and lower stem following treatment of various sized shoots with ^{14}C-glyphosate or ^{14}C-picloram. Expt. 3.3.2.3. 77

17. Retention of ^{14}C-herbicide by lanolin rings on leaves of Canada thistle. 80

List of Common Names and Designations of Chemicals

Common Name or Designation	Chemical Name
amitrole	3-amino-*s*-triazole
atrazine	2-chloro-4-(ethylamino)-6-(isopropyl)amino-*s*-triazine
benazolin	4-chloro-2-oxobenzothiazolin-3-ylacetic acid
bentazon	3-isopropyl-1*H*-2,1,3-benzothiadiazin-4(3*H*)-one 2,2-dioxide
bromoxynil	3,5-dibromo-4-hydroxybenzonitrile
chlorflurenol	methyl 2-chloro-9-hydroxyfluorene-9-carboxylate
2,4-D	(2,4-dichlorophenoxy) acetic acid
2,4-DB	4-(2,4-dichlorophenoxy) butyric acid
dicamba	3,6-dichloro-*o*-anisic acid
diuron	3(3,4-dichorophenyl)-1,1-dimethylurea
ethephon	2-(chloroethyl)phosphonic acid
glyphosate	N-(phosphonomethyl)glycine
MCPA	[(4-chloro-*o*-tolyl)oxy]acetic acid
MCPB	4-[(4-chloro-*o*-tolyl)oxy] butyric acid
oxamyl	methyl-N'N'-dimethyl-N-(methyl-carbamoyl)oxy-1-thiooxamimidate

paraquat	1,1'-dimethyl-4,4'-bipyridinium ion
picloram	4-amino-3,5,6-trichloropicolinic acid
POPOP	1,4-bis-2-(5-phenoxyloxazoyl)-benzene
PPO	2,5-diphenyloxazole
TEEPP	toluene:2-ethoxyethanol:PPO:POPOP,670:330:4:0.5, v/v/w/w.

1. INTRODUCTION

Canada thistle [*Cirsium arvense* (L.) Scop.] is a deep-rooted perennial weed which causes serious problems around the world. Due to its extensive creeping root system, Canada thistle is difficult to control. The best control of Canada thistle will be achieved when herbicides accumulate in the roots to toxic quantities. Herbicides that cause contact injury or possess poor translocation properties will not accumulate in the roots and therefore will not give satisfactory control. Herbicides with good translocation properties, applied at the bud or pre-bud growth stage of the thistle, have given excellent control. At these stages translocation of assimilate and, therefore, herbicides to the roots will be maximal as the plant begins to store carbohydrate reserves.

The requirement for weed control in the same season that a crop is seeded can present a problem. Herbicides must be tolerated by the crop if they are to be applied in mid-summer when the thistles are in the susceptible pre-bud stage. The potential to cause crop injury may still be present when using selective herbicides at an advanced crop growth stage in mid-summer. The use of non-selective, well translocated herbicides before the crop is seeded or after it is harvested would be ideal for thistle control without any crop damage.

Compared to mid-summer, basipetal translocation of assimilates and herbicides is less than ideal early and late in the season. Therefore, herbicides which are applied at these times should, in order to be useful, be effective even though basipetal translocation may not be maximal. Several herbicidal properties are required in order for a chemical to be effective when applied under less than ideal conditions. These may include persistence of the herbicide in the plant and translocation of the herbicide to all centres of plant growth and development.

Picloram and glyphosate are translocated, intact, to all portions of various species. The relative degree of their translocation in the xylem and phloem of different plant parts is not well known.

The present study was initiated in order to clarify some of these herbicidal properties. In earlier studies of herbicide translocation in perennial weeds, intact mature plants have been employed predominantly. Perennial weeds vary considerably from plant to plant and, therefore, in many instances only qualitative data have been reported for herbicide translocation. In this study an attempt was made to limit plant-to-plant variability by using two simple plant systems. These systems were the plant source-sink system and a previously unreported shoot-root system.

In the plant source-sink system, herbicide translocation was followed from a basal leaf (source) to the apex (sink). In addition, both systems were used to follow herbicide movement from tissue which normally acts as a sink for assimilates to other tissues in the plant. With the shoot-root system it was possible to quantitatively compare movement of the two herbicides from the shoot into the root tissue.

2. LITERATURE REVIEW

2.1 Biology of Canada Thistle

Canada thistle [*Cirsium arvense* (L.) Scop.] is a perennial weed found in all the temperate climates of the world. It was introduced into Canada from Europe in the 17th century. It now occurs in abundance in southern areas of Canada (102). Recent surveys indicate that infestations of this plant occur on 38, 23 and 57% of the cultivated land in Alberta, Saskatchewan and Manitoba, respectively (39, 153, 154).

Canada thistle cannot tolerate a lack or an excess of water (102). It does tolerate extremely high summer temperatures and it will survive winters where ambient temperatures go below -40 C. Under reduced lighting, poor stands can be expected (11).

Four varieties of Canada thistle have been described (103). In addition, many variations in morphology have been observed (68). These morphologically different 'ecotypes' of Canada thistle appear to have differential susceptibilities to herbicides (69, 70, 71, 127). Seeds of Canada thistle are viable under a variety of environmental conditions (165). Seedlings will quickly develop a tap root which will then produce lateral creeping roots. From the creeping roots or the original vertical root, rhizomatous shoots will develop (102). Seedlings which possess only two true leaves are able to resprout (8%) after clipping (165). The anatomy of the root structures has been described in detail (63).

Once established in a field, Canada thistle is able to regenerate from root sections. It is this vegetative reproduction from root sections that contributes greatly to the weedy nature of the species. Seeds are not cited as the primary means of spread of this perennial weed (11, 102). Working with 10-mm segments of root, Hamdoun (64) found that 25% of the segments would regenerate shoots. Larger root segments were able to produce shoots from greater soil depths (64). Canada thistle roots have been found at depths of 6 m (102). In addition to its extensive vertical growth, this plant can rapidly spread laterally (102).

By competing for moisture, nutrients and light, Canada thistle can severely reduce yields of cereal and oilseed crops. When dense infestations of Canada thistle were controlled, barley and canola (rapeseed) yields increased by over 300% (141, 142).

2.2 Perennial Weed Control

Despite continuing efforts, perennial weed problems in Western Canada have not decreased in the last 30 years (85). Estimated losses due to Canada thistle competition in Saskatchewan wheat in 1980 were 3.6 to 4.7 million dollars (116). A few explanations for the increases in perennial weed problems in agricultural soils have been suggested.

Crafts and Robbins (33) stated in 1962 that "the use of chemical weed control has led to the reduction of preventative weed control measures, such as tillage, fencerow clearing, crop rotation, etc." Similarly, Wyrill and Burnside (166) suggest that the increase in perennial weeds is due to "pre-emergence herbicide use or reduced cultivation". Whitwell et al. (163) also agree that the perennial weed, horsenettle (*Solanum carolinense* L.), has increased due to similar practices.

Most perennial weeds possess extensive underground structures such as tubers; rhizomes, bulbs or roots. These underground structures are able to store carbohydrates. Stored carbohydrates ensure that there is enough energy for new shoots to penetrate through the soil from great depths. Once a new shoot reaches the soil surface it is able to acquire its own energy.

Arny (8) monitored the root carbohydrate levels of five perennial weeds for one season. He found that total root carbohydrate levels reached a maximum at the pre-bloom stage for Canada thistle, sow-thistle (*Sonchus arvensis* L.), field bindweed (*Convolvulus arvensis* L.), Austrian field cress [*Rorippa austriaca* (Crantz) Bess.], and leafy spurge (*Euphorbia esula* L.). Welton et al. (162) found that mowing Canada thistle shoots before full bloom as compared to any other time, gave the greatest reduction in thistle shoots. Further control was obtained if thistle regrowth was cut every month, but no more often, until a killing frost. This practice reduced carbohydrate reserves to levels that were detrimental to winter survival and/or vigorous spring regrowth. This type of control method is not possible in cereal or oilseed crop situations without losing a cropping year to summerfallow.

With the advent of 2,4-D in 1941, selective suppression of broadleaf perennial weeds was possible in cereal and grass crops. Other phenoxy herbicides such as MCPA, 2,4-DB and MCPB followed. These herbicides were able to kill or stunt the foliage growth of perennial weeds if used early in the season for annual weed control. Later applications can result in mechanical damage to the crop from the application equipment, or crop injury can result if the applications are applied when the crop is in a herbicide-sensitive growth stage.

Devine (38) reported that 5% of foliage-applied ^{14}C-2,4-D was translocated to the roots of Canada thistle. Plant tissues metabolize 2,4-D quickly (131) and, consequently, even less than 5% of the unmodified 2,4-D would have reached the roots. Furthermore, compared to the herbicides picloram and glyphosate, 2,4-D is less phytotoxic on a molar basis. It is, therefore, not surprising to find that phenoxy herbicides such as 2,4-D are unable to give much more than top-growth control of Canada thistle.

Herbicides such as glyphosate, picloram, dicamba and amitrole are translocated to the roots in lethal quantities.

Not all of these chemicals can be used selectively in crops. Glyphosate, amitrole and picloram alone are used as broad-spectrum herbicides either before or after a crop or during a fallow year. Herbicides such as 2,4-D, MCPA, dicamba, bromoxynil and mixtures of 2,4-D and picloram continue to be used in Prairie field crops for Canada thistle control. In legumes, 2,4-DB and MCPB are recommended. Atrazine has been used in corn for effective season-long suppression of Canada thistle (21). Further chemical control of Canada thistle in various crops has been attained by bentazon in peppermint [(*Mentha piperita* (L.) Scop.)], benazolin in canola and mustard and recently 3,6-dichloropicolinic acid in canola (142) and strawberries (84).

The relative success of the above-mentioned herbicides in controlling Canada thistle depends to a large extent on the environmental and cultural conditions which accompany their use (6).

The growth stage at which the plants are treated is also important for successful control. All herbicides, including 2,4-D, perform optimally when applied at the early flower bud stage (6, 140). Similar to mowing or tillage at this growth stage, herbicide treatments will be suppressing Canada thistle when its capacity to regenerate is lowest.

In the greenhouse, several workers have attempted to increase the root bud activity of perennial weeds by trying to increase assimilate translocation to the roots. Carson and Bandeen (22) used ethephon in such an attempt. Ethephon applied simultaneously with 2,4-D or dicamba was the most efficient combination. McIntyre et al. (89) tried to increase root bud activity by exposing the root buds to high levels of nitrogen nutrition and apical shoot decapitation. They found increased translocation of ^{14}C-2,4-D to the roots under both conditions.

2.3 Translocation of exogenous and endogenous substances in plants

Plants are able to translocate assimilates from centres of production (sources) to centres of utilization (sinks). In addition, plants are able to translocate mineral ions and water from root hairs to all other parts. The mechanisms of translocation of assimilates, water and mineral ions have been covered in recent manuscripts (88, 115, 171).

In order to describe translocation, the plant is usually divided into two basic parts. These are the symplast and apoplast. The symplast is defined as "the continuum of interconnected protoplasts of the plant" (32). The apoplast is the "continuum of non-living cell wall material that surrounds and contains the symplast". Phloem sieve tubes, sieve elements and companion cells are regarded as the symplast. Xylem vessels and tracheids as well as intercellular spaces are considered as integral parts of the apoplast. A plasmalemma that is selective as to the compounds which may permeate it, separates the apoplast and symplast.

Most pesticides, assimilates, mineral ions and some endogenous plant compounds are able to move readily in the symplast and/or apoplast. Compounds which are able to traverse the plasmalemma freely, can be found in both the symplast and apoplast at any one time.

Assimilate translocation is generally believed to be from source to sink via the phloem. For example, the results of many studies illustrate the movement of assimilates from their centre of production in the leaves to metabolically active centres in the storage roots and stems and in root and leaf apices (18, 52, 83, 159).

The assimilates identified in most studies are generally transport sugars (sucrose, galactose-containing oligosaccharides, etc.) (56). These sugars are selectively retained in the phloem tissue. The expenditure of energy is generally believed to be necessary for the loading of these sugars into the phloem (114).

In studies using assimilates produced from $^{14}CO_2$, up to 1% of the labelled assimilates are amino acids and other endogenous plant products (113). The amide amino acids (arginine and glutamine) are able to move freely between the xylem and the phloem (13, 113). This ensures that organic nitrogen is circulated throughout the plant to both transpiration sinks (mature leaves) and metabolic sinks (metabolically active young tissue and roots).

The translocation of abscisic acid, gibberellins, cytokinins and auxins has been reviewed by Ziegler (170). All of these compounds have been found in the phloem. Auxins move slowly from cell to cell, both acropetally and basipetally, in plants (13). From their centre of production in the young tissue, gibberellins are believed to move passively in both the phloem and xylem. Cytokinins are not translocated in the plant as readily as auxins and gibberellins. Cytokinins are produced in the roots and are translocated in the xylem to the stem and foliage. They appear to have very little phloem mobility.

The uptake of mineral ions by roots is thought to require energy, although this is disputed (115). Once in the xylem system of the root, mineral ions may move acropetally in the transpiration stream. Although initially transported in the xylem, many inorganic ions (K^+, Rb^+, Cs^+, Na^+, Mg^{2+}, Cl^-, PO_4^{2-}, SO_4^{2-}) are commonly found in the phloem (170). Potassium and chloride ions are known to transfer between the xylem and phloem quite readily. Whether the other ions transfer readily across the plasmalemma or are actively transported across the plasmalemma in the mature leaves, is not known. The inorganic ions, Ca^{2+} and B^{2+}, are not found in the phloem (170).

The movement of pesticides in the plant is analogous to the movement of one or more of the natural plant compounds already mentioned. The translocation of ^{14}C-labelled assimilates and herbicides has been compared in a number of studies (27,48,50,54).

Pesticides can be classified into three categories according to their translocation characteristics. Chemicals that are transported with the transpiration stream and accumulate at leaf edges, after being introduced to the plant via the roots or foliage, were at one time all regarded as apoplastic. It was believed that apoplastically transported pesticides did not readily enter the symplast. Yet, in order to cross the Casparian strip and reach the root xylem, they must enter the symplast. Evidence has been presented to show that many apoplastically transported pesticides will move freely from the apoplast to the symplast (43). Since the xylem stream moves at speeds up to a hundred times greater than those of the phloem, these chemicals will tend to be retained and translocated in the transpiration stream (43,156). Edgington and Peterson (43) have termed pesticides which move apoplastically in the plant, yet are able to cross the plasmalemma into the symplast, as pseudoapoplastic. No pesticide has been reported to be unable to traverse the plasmalemma, although some dyes do possess truely apoplastic characteristics and will not traverse the plasmalemma (117).

The substituted *s*-triazines and ureas are examples of pseudoapoplastic pesticides. They are transported predominantly in the transpiration stream, but have been shown to rapidly cross the plasmalemma (117). Since they move in the transpiration stream, any increase in the transpiration rate will also increase the acropetal translocation rate of these herbicides (66,144).

Pesticides that move in the symplast after a foliage application are deemed symplastic. Symplastic pesticides will move in the plant with assimilates to metabolically active centres. A classic example of a herbicide which moves with assimilates is 2,4-D (125). The distribution patterns of ^{14}C-2,4-D and ^{14}C-assimilates are similar to each other in grasses and broadleaved plants, although quantities of 2,4-D translocated to the roots are generally less than those of assimilates (110).

Symplastic herbicides when applied to roots via nutrient solution will move in the apoplast. It is also possible for them to be retranslocated in the phloem from transpiration sinks (55), whereas apoplastic herbicides cannot be retranslocated via the phloem.

A pesticide capable of moving in both the symplast and apoplast as well as being able to move freely in both directions across the plasmalemma has been called ambimobile (118). Glyphosate is ambimobile. It has been shown to move in both the symplast and the apoplast (149). It can also leak out of the phloem into the transpiration stream at a rate much greater than that of ^{14}C-assimilates (40). This free movement of glyphosate in the symplast and apoplast ensures that it reaches both transpiration and assimilate sinks throughout the plant. Many other pesticides are ambimobile to varying degrees (98).

What are the chemical characteristics required of a pesticide before it can be considered symplastic, apoplastic or ambimobile? These characteristics are generally not known. Crisp (35) has developed the hypothesis that all chemicals that are weak acids or can be converted to a weak acid in the plant, are symplastic. He reasons that a weak acid containing a carboxyl group is in a non-polar, undissociated form in the slightly acidic apoplast. In this form it is able to diffuse across the plasmalemma that separates the symplast and apoplast. Once in the phloem sap with a pH 7.5, the molecule becomes dissociated, hydrophilic and unable to pass back through the largely lipophilic plasmalemma.

Active transport of some symplastic pesticides across the plasmalemma cannot be overlooked. If active transport does play a dominant role then herbicides, once in the phloem, would not be able to reach the xylem without the expenditure of energy by the plant in addition to that required to initially enter the phloem.

In order to explain the ambimobile nature of the nematicide, oxamyl, which is not a weak acid and has not been shown to be actively transported, another theory was developed by Peterson et al. (118). This theory suggests that the diffusion of a chemical through the plasmalemma would be great enough to allow passive permeation from the sieve cells to the apoplast. On the other hand, this passive permeation would be small enough to permit phloem translocation of the chemical through the plant (156). Glyphosate has been shown to possess the properties necessary for this slow-diffusion theory (59,98).

An ambimobile herbicide has the properties required for a superior systemic pesticide (43). It can be transported out of the treated leaf via the phloem and reach the roots and leaf and shoot apices. Apoplastic transport in the xylem would ensure that the herbicide reached mature leaves. Ideally, all tissue in a treated plant would be exposed to an ambimobile herbicide.

As the translocation of natural plant compounds is altered by the environment, so will that of exogenously applied chemicals. When assimilate translocation to the roots of perennial weeds is greatest, the translocation of herbicides is also greatest (53,72).

Pesticides can affect their own distribution pattern and translocation rate by killing or causing injury to the living sieve tube cells in which they are moving. Few studies have been completed in the area of herbicide-induced inhibition of their own translocation. Sharma and Vanden Born (138) reduced assimilate translocation in barley and Canada thistle with picloram. Studies with grape vines indicated that picloram and 2,4-D were able to inhibit assimilate translocation (86). In the field, high rates of herbicide have resulted in reduced control of regrowth (71), probably because the herbicide killed translocation tissue and therefore reduced its own translocation to the roots.

Induced stress also can alter normal translocation rates and sinks in plants. Dewey (40) created artificial sinks and found both glyphosate and ^{14}C-assimilates to respond by being translocated to the artificial sinks. Water stress and low humidity have reduced the translocation of both apoplastically and symplastically transported herbicides (12,111). Other factors that influence transport of pesticides in plants are light intensity, temperature, metabolic inhibitors and defoliation (89,97,144). Many of these may actually exert their causal effect on phloem loading or root uptake as opposed to limiting actual transport (38,144,145).

When performing translocation studies with leaf-applied materials on whole plants, phyllotaxy must not be neglected. Depending on the phyllotaxy of the experimental plant, certain leaves, bulb scales, fruit sections, etc. will receive more ^{14}C-labelled assimilates or pesticides than others (126,155). This is due to a more direct vascular route between the plant tissues where translocation is greatest.

2.4 Picloram

Picloram (4-amino-3,5,6-trichloropicolinic acid) was introduced in the early 1960's for the control of broadleaved weeds and brush. Many weeds not controlled with 2,4-D could be eliminated from crop and non-crop areas by the use of this herbicide. Of additional importance is the ability of picloram to eliminate or substantially suppress various perennial weeds that were formerly difficult to control with the cultural and chemical methods available (5).

Due to the persistence of picloram in soil, picloram is able to give season-long control of susceptible weeds. This persistence has also led to the problem of soil residues in succeeding years. On the Canadian prairies there is a reported dissipation rate for picloram of 32 to 45% per year (78,158). In years following picloram application, soil residues may cause adverse effects to susceptible crops such as legumes, sunflower and canola. In some years, picloram soil residues have also reduced wheat yields (78).

Picloram is not readily metabolized by plant tissue. No ^{14}C-picloram was metabolized by Canada thistle, soybeans or barley within a period of 20 days(139). Loss of ^{14}C-picloram through decarboxylation from the leaf surface of the above plants was reported to be only 0.5% of the applied dose (139).

Abnormalities induced by picloram in plants susceptible to picloram include callus formation, adventitious roots, root swelling and epinasty (47). Necrosis can occur on the treated leaves. These symptoms are very similar to those caused by 2,4-D. Symptoms induced by picloram appear more rapidly than those induced by 2,4-D (133).

The mechanism of selectivity and mode of action of picloram are believed to be similar to those of other auxin-like herbicides. Malhotra and Hansen (94) found the quantity of RNA, DNA and protein to increase in treated plants. Later studies proved these changes to be due to increased cell division and RNAase and DNAase activity (122). Similar biochemical changes have been observed after treatment with 2,4-D (9).

Meristematic activity in the procambium of ironweed (*Vernonia baldwini* Torr.) increased until the primary phloem was obliterated (133). Such phloem destruction after treatments of picloram has also been observed by other researchers (47,82).

The destruction of the phloem may explain the reduced translocation of picloram to roots of perennial weeds as compared to 2,4-D (60). It may also explain the inhibition of ^{14}C-assimilate translocation to the roots after picloram treatment of grapes (86) and Canada thistle (138). In comparison to the phloem the xylem is relatively unharmed by picloram (82).

Picloram may enter a plant either by root uptake or by foliar or stem absorption. The foliar absorption of picloram was slightly less than that of 2,4-D amine in aspen poplar (*Populus tremuloides* Michx.) (137) and Drummond's goldenweed [*Isocoma drummondii* (T. & G.) Greene] (99). Under optimum leaf uptake conditions (for example, with high humidity and surfactants added to the treatment solution) or with increased time this difference was reduced (136). The uptake of picloram by Canada thistle was 16% of the applied dose within 24 hours (136).

Once taken up by the leaf tissue, picloram will move out of the treated leaf to the remainder of the plant. In Canada thistle and barley, Sharma (135) observed that up to 35% of the applied dose was translocated out of the treated leaf in 4 days. Within 24 hours of applying picloram to a source leaf, it was found distributed throughout Canada thistle plants (136). Rapid translocation of picloram in plants has also been noted by other researchers (17,65). Picloram translocation was greatest at a temperature of 29 C in combination with long days (121), remained unchanged with the addition of ammonium sulphate to the spray solution (164) and was reduced under extreme moisture stress (101).

Translocation of picloram to the roots has been noted as one of the necessary factors for perennial weed control. The translocation of lethal quantities of picloram to the roots of Canada thistle has been observed (135,136). Similar observations have been made for field bindweed (3), huisache [*Acacia farnesiana* (L.) Wild.] (17), skeleton weed (*Chondrilla juncea* L.) (60) and Drummond's goldenweed (99).

The tissue concentration of picloram necessary for root kill has been estimated to be 0.3 ppm on a fresh weight basis (17). Even with picloram-induced destruction of the phloem, these minute quantities of picloram were able to reach the roots of skeleton weed (60).

The root uptake and translocation mechanism of picloram has been reported to be a complex combination of physical and metabolic processes (107). Gaudiel and Vanden Born (55) have shown that in young soybeans approximately half of the picloram which accumulated in the apex arrived directly via the stem xylem from the roots. The other half was carried in the transpiration stream to the mature leaves and was then re-transported in the phloem to the metabolically active apex. Crafts and Yamaguchi (34) have stated that the ability of a foliage-applied herbicide to cross the membrane between the apoplast (xylem) and symplast (phloem) is related to its ability to efflux from the roots. Less than 0.5% of foliage-applied picloram was exuded from roots of Canada thistle (136) and skeleton weed (60).

Picloram mobility in plants can be attributed to some of its chemical properties. Picloram has a low pKa value (3.8) and is a weak acid, characteristics that are needed for phloem mobility according to the Crisp weak acid theory (35). In other studies, picloram was found to leak out of potato tuber tissue at rates similar to those required to fit the Edgington-Peterson slow-diffusion theory for ambimobility (152).

In summary, picloram will move in the symplast, apoplast, across the membranes between the symplast and apoplast and will subsequently become distributed throughout the tissues of most plants (46,55). These are characteristics of a successful ambimobile herbicide.

2.5 Glyphosate

Glyphosate [N-(phosphonomethyl)-glycine] has been used successfully and extensively since its introduction as a broad-spectrum, post-emergence herbicide in the early 1970's.

Residues of glyphosate in the soil are practically negligible (44,147,148). In most instances, fields may be sprayed immediately prior to crop emergence without phytotoxicity to the crop. Rapid inactivation in the soil has been attributed to the binding of glyphosate to clay particles and ferric, ferrous and aluminum ions (30,67,148).

Glyphosate has shown no detrimental effects on a variety of water and soil flora and fauna (30,96). Indeed, after glyphosate is bound to soil it is quickly degraded in the soil to carbon dioxide through the action of microorganisms (108).

Glyphosate demostrates very little selectivity between plant species. Consequently, glyphosate provides excellent control of a vast variety of weeds, including deep-rooted perennial plants (15,28,36,37,44,58,169). The weed control obtained with the use of glyphosate has repeatedly been reported to be superior to that obtained with other herbicide treatments (45,112). A few perennial plants that show some tolerance to glyphosate are leafy spurge, field bindweed, field horsetail (*Equisetum arvense* L.), hemp dogbane (*Apocynum cannabinum* L.) (166), Norway spruce (*Picea abies* L.) and Scotch pine (*Pinus sylvestris* L.) (87).

Leafy spurge tolerance has been attributed to less retention of the herbicidal spray by the foliage of this plant (58). Similar conclusions have been drawn for field horsetail tolerance to glyphosate (36). Alternatively, inadequate translocation has been cited for the incomplete control of field bindweed (128).

Marginal selectivity in some crops has been attained with carefully timed applications (37,74,95,143). Further selectivity has been acquired with the use of novel directed application methods (7,16,92) that take advantage of the unique translocation properties of glyphosate. From a single application site, glyphosate will translocate throughout the plant in lethal quantities.

Except in the special cases mentioned above, selective use of glyphosate in crops has not been possible. Therefore, the control of perennial weeds in cropland must be completed before the emergence of the crop (168), immediately before harvest (10,109) or after harvest (37). When glyphosate is applied before crop emergence or after crop harvest, the low vigour or inadequate growth of the target plant may limit control.

Sprankle et al. (149) first reported on the translocation of glyphosate to metabolic sinks of the shoot apex, leaf blade apex, root tip meristem, storage roots and tubers and root and leaf buds. Many later reports also have acknowledged these translocation phenomena of glyphosate (14,28,45,76,87,95,128,131,166,169). Most researchers agree that for glyphosate to reach the metabolically active centres it must move in the plant symplast.

In addition, however, autoradiographs showed the occurrence of glyphosate at leaf margins (14,58,87,149,166). This is indicative of apoplastic transport (106).

Translocation rates for glyphosate are high. Glyphosate was translocated to the roots of common milkweed (*Asclepias syriaca* L.) at rates up to four times greater than those of 2,4-D (166). Devine (38) found 2,4-D less mobile than glyphosate in Canada thistle. Four hours after treatment, 11 and 52% of the applied glyphosate was found in the roots of reed canarygrass (*Phalaris arundinacea* L.) and creeping red fescue (*Festuca rubra* L. var. *rubra*), respectively (95).

Attempts have been made to stimulate root bud activity of perennial plants with the expectation that the flow of assimilates to the roots will increase. Consequently the transport of herbicides to the roots would also increase (23,24,25). In one year of results, chlorflurenol, tank-mixed with glyphosate, reduced Canada thistle regrowth 19% more than glyphosate alone (80). Whether these results are due to increased leaf uptake or penetration of glyphosate or whether the plant growth regulator actually stimulated root buds and subsequent glyphosate translocation is unknown.

The growth stage at which various plants are treated is important to the ultimate control of the plant. When assimilates are translocated from the roots to the shoots in the spring little or no glyphosate will be translocated in the opposite direction to the roots. Increased perennial weed control with foliage-applied herbicides has been observed at growth stages when assimilates are being translocated to the roots. This appears to be the 4 to 5 leaf stage in quackgrass [*Agropyron repens* (L.) Beauv.] (28,48,50,124) and the late bud stage in Canada thistle (57,77,140).

The absorption and translocation of glyphosate from foliage has been reported to reach a maximum after 3 days for hemp dogbane (131), hedge bindweed (*Convolvulus sepium* L.), field bindweed and Canada thistle (128). No data have been reported to indicate when foliar absorption in plants is complete. It is possible that absorption continues until the treated foliage becomes chlorotic and necrotic (131). Foliar absorption was greater from the upper leaves of hemp dogbane than from the lower leaves (131). These younger leaves probably have less hydrophobic epicuticular wax and, therefore, glyphosate absorption would be greater from their surface.

Compared to other herbicides, glyphosate absorption has tended to be less in various plant species (131). This is probably due to the greater hydrophilic nature of glyphosate. The fairly polar molecules of glyphosate would encounter considerable difficulty in crossing the largely hydrophobic leaf waxes (130). The use of surfactants with glyphosate has increased leaf uptake and glyphosate activity in several plant species (58,75,90).

Several environmental factors have been reported to increase or decrease the activity of glyphosate in many plants. Most of these studies did not partition the portion of increases or decreases of toxicity due to absorption or translocation. Toxicity does increase with greater relative humidity (26,58,75,90). By analyzing the amount of ^{14}C-glyphosate remaining on the leaf surface, Gottrup et al. (58) and Jordan (75), concluded that absorption had significantly increased under high humidity. Several authors have reported increased quantities of ^{14}C-glyphosate in roots and rhizomes distant from the treated leaf under high humidity (26,58,75,90,163).

Decreased activity has been correlated with moisture stress in the treated plant (4,26,90,104). Chase and Appleby (26) concluded that translocation, and not absorption, was decreased under moisture stress.

Lack of light has been deemed responsible for delay in glyphosate activity (2). Furthermore, the presence of light has improved the translocation of glyphosate to the roots (76). On the other hand, too much light (75 klux compared to 50 klux) has been found detrimental to the basipetal translocation of ^{14}C-glyphosate in hydroponically grown hemp dogbane (131). High light intensities could cause increased necrosis and ultimately decreased glyphosate absorption (131). Alternatively, light energy could increase active uptake of glyphosate (163). Since glyphosate is believed to move mainly with assimilates in plants any increase in mobile assimilates through increased light energy could also increase the translocation of assimilates and glyphosate.

Temperature can also vary the efficacy of glyphosate. A temperature of 35 C has been found inhibitory to glyphosate activity. Such inhibition was greater when relative humidity was low and surfactant was not included in the spray solution (23,75,90,91). The extent of ^{14}C-glyphosate absorption and translocation under different temperatures has not been consistent (75,91). Evans (44) has stated that colder weather may slow down initial glyphosate phytotoxicity, but regrowth control may improve.

There have been some unaccountable observations with regard to glyphosate translocation. In studies involving Canada thistle, Gottrup (57) found that some shoots along a section of root were by-passed while terminal shoots contained up to 6% of the total ^{14}C-glyphosate applied to the plant. Claus and Behrens (28) observed a similar phenomenon in quackgrass. These studies could simply illustrate that the buds proximal to the mother shoot are under the apical dominance of the mother shoot. Those shoots distal from the mother shoot may have been released from apical dominance. The distal buds and shoots which have escaped apical dominance will receive assimilates and, therefore, herbicides from the mother shoot. This assimilate supply will continue until they develop their own independent nutrient supply. Apical dominance studies on aspen poplar roots have indicated similar conclusions (129).

Unlike soil microbes, plants are unable to break down glyphosate quickly. Metabolism of glyphosate in the following species has been reported to be negligible: Canada thistle and leafy spurge (58), purple nutsedge (*Cyperus rotundus* L.) (169), common milkweed and hemp dogbane (166), tall morning glory [*Ipomoea purpurea* (L.) Roth.] and field bindweed (128), creeping red fescue and reed canarygrass (95).

In 1972, Jaworski (73) claimed that glyphosate inhibition of *Lemna gibba* L. and *Rhizobium japonicum* (Kircher) Buchanan was partly alleviated by the addition of phenylalanine and tyrosine. Many later reports have verified that the addition of phenylalanine and tyrosine can alleviate some or all glyphosate inhibition (61,62,134).

In general, glyphosate appears to slow down several metabolic processes, and increase the breakdown of intracellular ultrastructures (20,119,157), yet it has no known effect on the permeability of membranes (19,49,123). It is also undoubtedly involved with aromatic amino acid biosynthesis or metabolism (42).

3. MATERIALS AND METHODS

3.1 Plant Material

3.1.1 Whole Plant Studies

Canada thistle shoots were propagated in vermiculite from root cuttings taken originally from one plant. Root cuttings were transplanted into an unsterilized clay-loam soil:peat (4:1) mixture. They were then grown for 6 to 8 weeks in the greenhouse. The greenhouse daylength was extended to 16 hours with 80 $\mu E.m^{-2}.s^{-1}$ of artificial lighting from fluorescent and incandescent lamps (measured with a Li-Cor quantum meter, Model Li-185; Lambda Inst. Corp., Lincoln, Nebraska.)

One week before herbicide treatment, plants were transferred to a growth cabinet with a 16-hour day, 25 C day, 21 C night and a photon flux density of 220 $\mu E.m^{-2}.s^{-1}$ supplied from fluorescent and incandescent lamps. One day prior to treatment, plants were trimmed to a simple source-sink system consisting of a green basal leaf and the apical shoot (Figure 1). Plants in bud were not used. Within each replicate, plant sizes were similar and the number of leaves removed between the basal leaf and the apex was constant (8 to 17 leaves).

3.1.2 Shoot-Root Studies

Long sections of root (30 to 40 cm) were obtained from 10 to 20-week old plants, grown in the greenhouse. These sections were pruned of all secondary roots and buds and placed in a shallow tray of vermiculite for 1 to 2 weeks. When shoots appeared, roots were cut into 20-cm segments with the newly emerged shoot at the end proximal to the former mother shoot (Figure 2). Replicates were made up from root segments of similar size. Roots were placed at a depth of 5 cm in vermiculite in shallow trays. Future references to "shoot" with regard to all shoot-root experiments, denote all the leaves and apex with their attached stem. Similarly, references to "lower stem" denote the vertical stem tissue from the horizontal root to the lowest leaf. This lower stem usually was 5 to 7 cm in length.

3.2 Radioactive Chemicals

Radioactive N-(phosphonomethyl)glycine (^{14}C-glyphosate; specific activity 426 kBq/mg) was obtained from Monsanto Co. (St. Louis, Missouri). It was labelled at the carbon atom adjacent to the phosphorus. The parent acid was converted to the monoisopropylamine salt, by the addition of isopropylamine in a 1:1 (v/v) ratio. The salt was diluted with a commercial formulation of glyphosate (Roundup) and sterilized water to produce a treatment solution for the whole plant studies with a radioactivity of 370 Bq/μl and a

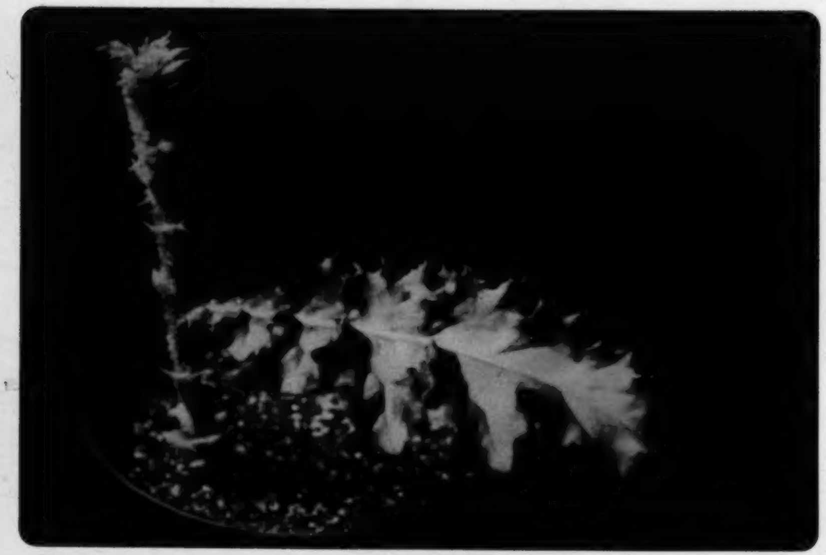

Figure 1. Canada thistle source-sink plant systems used in Experiments 3.3.1

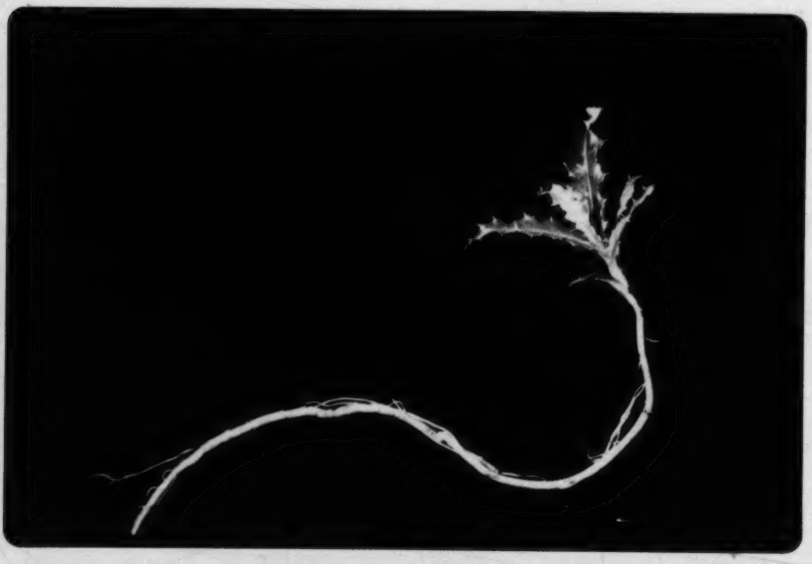

Figure 2. Canada thistle shoot-root plant system used in Experiments 3.3.2

glyphosate concentration of 5.2 ug/ul. The radioactivity of the treatment solution for the shoot-root studies was 170 Bq/ul with a glyphosate concentration of 2.4 ug/ul.

Radioactive 4-amino-3,5,6-trichloropicolinic acid (^{14}C-picloram; specific activity 1.53 x 10^3 kBq/mg and 158 kBq/mg) was obtained from Dow Chemical Co. (Midland, Michigan). It was labelled at the carboxyl position. The original 99% pure crystal was dissolved in 95% ethanol. The final treatment solution for the whole plant studies had a radioactivity of 379 Bq/ul and a picloram concentration of 2.35 ug/ul. The treatment solution for the shoot-root experiments differed in that the picloram crystal was dissolved in 70% ethanol and mixed with a commercial formulation of picloram (Tordon 22K) to a picloram concentration of 2.4 ug/ul. This solution had a radioactivity of 370 Bq/ul. Atplus 411F adjuvant (83% paraffin oil and 17% non-ionic ethoxylated ester surfactant; Atkemix Inc., Brantford, Ontario) was added to both treatment solutions to a final concentration of 0.7% v/v.

Barium ^{14}C-carbonate with a specific activity of 940 kBq/mg was purchased from New England Nuclear (Boston, Mass.). Two mg (1.88 x 10^3 kBq) of $Ba^{14}CO_3$ powder was placed in a 20-ml glass vial. The vial was then placed inside an airtight assimilation chamber. Carbon-14-labelled carbon dioxide was generated by introducing 3 ml lactic acid through a stopcock. A small fan inside the assimilation chamber assisted in circulating the $^{14}CO_2$.

3.3 Treatment of Plant Material

3.3.1 Whole Plant Studies

To the basal leaf or apex of each plant, 20 ul of herbicide treatment solution (7.6 kBq picloram or 7.4 kBq glyphosate) was applied. The treatments were applied at hour 6 of a 16-hour day. The basal leaf application was to the midvein inside a lanolin ring. The apex application was to the oldest leaves in the apex. A lanolin ring was not used for the apex application. The treated tissue (apex or basal leaf) was enclosed in a plastic bag for the duration of the experiment to increase the humidity. After harvest, plants were divided into the tissues to be analyzed. All harvested tissue was weighed fresh.

The treated foliage, apex or basal leaf, was rinsed with 50 or 10 ml of solvent, respectively. A thimersol antibacterial solution [1 g thimersol (sodium ethyl mercuric thiosalicylate)/ L distilled water] and 95% ethanol were used as solvents for glyphosate and picloram, respectively. Aliquots of the leaf rinses were taken immediately and assayed by liquid scintillation spectrometry. All plant tissue was stored in a freezer at -15 C until extracted or freeze-dried and combusted. Lanolin rings were removed from leaves after the tissue was frozen.

In the whole plant studies with ^{14}C-assimilates, only basal leaves were exposed to $^{14}CO_2$. This was accomplished by inserting the basal leaf through an opening in a

12 x 12 x 24 cm plexiglass assimilation chamber. The chamber was located in a fumehood under incandescent lamps that produced a photon flux density of 200 $\mu E.m^{-2}.s^{-1}$.

Twenty-four hours prior to $^{14}CO_2$ release, leaves of three new plants were introduced into the chamber and the chamber was sealed around the leaf petiole with Terrostat caulking (Terosan GmbH, Heidelberg, Germany) and vacuum grease (Dow Corning Corp., Midland, Michigan). The beginning of $^{14}CO_2$ release corresponded to hour 6 of a 16-hour day. Plants were allowed to photosynthesize in the $^{14}CO_2$ atmosphere for 3 hours. The chamber was then flushed through 4N KOH traps for 2 hours. The plants were carefully removed from the chamber, rinsed with water, and placed in the growth cabinet used for the herbicide treatments. The three plants from each treatment period were subsequently harvested at three different times. Harvested plants were separated into the tissue to be analyzed in a manner similar to that for the plants treated with herbicide.

3.3.1.1 The Absorption and Translocation of ^{14}C-glyphosate and ^{14}C-picloram from Basal and Apical Leaves

Using the whole plant source-sink system, the uptake and subsequent translocation of ^{14}C-picloram and ^{14}C-glyphosate was studied from the basal leaf and apical leaves. Plants were treated with 20 μl of the treatment solutions (7.4 kBq, 0.1 mg glyphosate; 7.6 kBq, 0.05 mg picloram). The experiments were repeated once with five replicates each time. The two herbicide treatments were completed at different times.

Plants were harvested at 1, 3 and 7 days after treatment. The plant parts analyzed for ^{14}C-activity included the treated leaf wash, apex, basal leaf and intervening stem. Due to the difficulty in separating all the roots from the soil, roots were not examined for ^{14}C-activity.

3.3.1.2 Basipetal Transport from the Apex

From this experiment an assessment of the amount of ^{14}C-herbicide translocated out of a treated apex to different portions of the plant stem could be made. Five replicates of plants treated with 20 μl ^{14}C-picloram or ^{14}C-glyphosate treatment solution were harvested 3 days after treatment. Tissues analyzed for radioactivity were the apical leaves (with no leaf rinse), the basal leaf and the intervening stem divided into three equal parts.

3.3.1.3 The Translocation of ^{14}C-assimilates from a Basal Leaf Exposed to $^{14}CO_2$

The $^{14}CO_2$ treatment methods are described under radioactive chemicals (Section 3.2). The tissues analyzed for radioactivity in this experiment were the same as in Experiment 3.3.1.1 except that the lower stem (soil level to basal leaf) was also analyzed for radioactivity. Plants esposed to $^{14}CO_2$ on the same day were harvested at different times, viz. 1, 3 and 7 days after $^{14}CO_2$ exposure.

3.3.1.4 The Effect of Girdling on Acropetal and Basipetal Translocation

By steam-girdling the stem below the basal leaf, the sink in the roots for assimilate and herbicide originating in the basal leaf or apical leaves would be removed. By comparing the girdled plants to plants in which the stem was not girdled, the effect of removing the root sink on basipetal and acropetal movement of the herbicide in the plant could be evaluated.

Twenty μl ^{14}C-picloram treatment solution (3.6 kBq) was applied to the apical leaves or basal leaf of each source-sink plant system. Half of the plants were steam-girdled on the main stem below the basal leaf. There were five replicates in the experiment. All plants were harvested 3 days following treatment and the tissues analyzed for radioactivity were the leaf washes, the apex, the basal leaf and the intervening stem.

3.3.1.5 Translocation of Non-radioactive Chemicals Past a Petiole Girdle

A girdling experiment was also completed using non-radioactive herbicides. Plants were trimmed to a basal leaf and an apex as in the preceding experiments. There were four replicates. Herbicides were applied inside a lanolin ring on the basal leaf. Treatments included an untreated control; picloram, and glyphosate, on plants with the basal leaf petiole intact or steam-girdled. Herbicide treatment solutions were made from commercial formulations. The concentrations of the treatment solutions were 2.88 mg ai glyphosate/ 40 μl and 1.56 mg ai picloram/ 40 μl. Girdling of the basal leaf petiole and the application of the lanolin ring was done 1 day prior to the herbicide treatment. Plant mutilation was completed 2 days before treatment. Filter paper was placed beneath treated leaves to prevent subsequent soil contamination.

Observations were taken throughout the experiment. The degree of chlorosis and necrosis on all plant leaves was noted. Four times during the experiment the number of leaves, greater than 4 cm in length, present in the apex was recorded. After 22 days, plants were harvested and fresh and dry weights of the apical leaves and their adjoining stem were taken.

3.3.2 Shoot-root Studies

3.3.2.1 Shoot-root Mutilation Studies Involving a Series of Doses of Glyphosate and Picloram

Experiments using the shoot-root system were initially conducted using non-radioactive herbicides. In these experiments, shoots were treated with a series of herbicide doses and observations on the ability of the herbicide to prevent further shoot and root growth were taken. There were four replicates of all treatments.

Treatment solutions of picloram and glyphosate at concentrations of 0, 0.5, 1.0, 2.0, and 5.0 mg ai/100μl were applied to leaves of the young shoots. These solutions were made from commercial formulations of glyphosate (Roundup) and picloram (Tordon 22K). For each treatment combination plants were divided into two equal groups. Shoots were severed from the roots on day 1 for the first group and on day 3 for the second group. From the experiment the affect of herbicide dose and the time required for a lethal amount of herbicide to be translocated into the root tissue could be observed. Roots were considered dead if they were rotted. Observations were taken up to 30 days following treament.

3.3.2.2 Translocation of Shoot-applied ^{14}C-glyphosate and ^{14}C-picloram into the Root Tissue

The three largest leaves of each shoot were treated with 20 μl of treatment solution containing 0.048 mg glyphosate (3.4 kBq) or 0.04 mg picloram (7.4 kBq). A sheet of plastic covered all treated plants in order to obtain a high humidity. The glyphosate and picloram treatments were not completed at the same time.

The experiment was conducted in order to follow the movement of both herbicides into the root over a period of 8 days. Plants were harvested at 2, 6, 26, 30, 74, 98, 146 and 194 hours following treatment. Harvested plants were divided into the shoot and the lower stem and the root was divided into three equal parts, RT1, RT2, RT3, with RT3 being distal to the stem and shoot. Treated leaves were not rinsed at harvest. All separated plant tissue was frozen at -15 C until extraction.

3.3.2.3 Effect of Shoot Size on Herbicide Translocation into Root Tissue

It was of interest to determine whether the size of the above-ground shoot had any effect on the amount of shoot-applied herbicide translocated to the roots. Small shoots were 3 to 5 cm high with 4 to 6 leaves. The larger shoots were 6 to 13 cm high with 8 to 14 leaves. The larger plants were 4 weeks old, compared to 1 week for the smaller plants. Plants were treated with 0.04 mg picloram (7.4 kBq) or 0.048 mg glyphosate (3.4 kBq) and harvested 3 and 9 days following treatment. Fresh weights of the shoots were taken.

3.3.3 Retention of Herbicides by Lanolin Rings

The ability of lanolin to retain the herbicides glyphosate and picloram was examined. Lanolin was removed from the frozen leaves of plants in Experiment 3.3.1.1. The rings were placed in 50-ml beakers and dissolved in benzene. After the benzene evaporated, lanolin remained on the bottom as a thin layer. This lanolin was redissolved in 10 ml benzene. Aliquots of benzene-dissolved lanolin (1 ml) were quickly added to 15 ml of TEEPP fluor and counted by liquid scintillation spectrometry. There was no attempt made to idenitify the compounds accounting for the ^{14}C-activity.

3.4 Determination of Radioactivity in Plant Tissues

3.4.1 ^{14}C-glyphosate

All plants treated with ^{14}C-glyphosate were analyzed for ^{14}C-compounds in the same manner. Tissue was ground in an Omnimixer (Ivan Sorval Inc., Newtown, Conn.) or a

Polytron (Brinkman Inst., Rexdale, Ontario), depending on the amount of tissue to be ground, with 20 to 100 ml of thimersol solution. Ground tissue was shaken for 3 hours and then centrifuged at 520*g* for 30 minutes in graduated centrifuge tubes. Aliquots (1, 2 or 4 ml) were added to 15 ml of Aquasol, a xylene-based scintillant (New England Nuclear).

The extraction procedure was 88.2 ± 3.1% ($s_{\bar{x}}$) efficient at recovering ^{14}C-activity from plants treated 3 days previously. Radioactivity in the residue material was negligible. This was tested by comparing the ^{14}C-activity in the aliquots of supernatant to the ^{14}C-activity remaining in known volumes of residue (the residues were freeze-dried and then combusted; see Section 3.4.2). The correlation between these two values was 0.951 and was significant (p=0.01).

The metabolism of ^{14}C-glyphosate in plants has been reported to be negligible (38,58,131). This was confirmed in the present study by two different procedures of thin-layer chromatography. Pooled extracts from the stem, apex and basal leaf following basal leaf treatment and the apex following treatment of the apex were filtered, freeze-dried and redissolved in a small volume of distilled water. Plates were spotted with 50 μl of the concentrated solutions.

The ethanol eluant for procedure one is described by Sprankle et al. (150), solvent system I. It was run on plastic-backed cellulose 13255 plates (No. 6004, Eastman Kodak Co., Rochester, New York) for 3 hours. The phenol and semi-stench eluants for procedure two are described by Putnam (120). Plastic-backed plates tended to dissolve in the phenol eluant. Consequently, glass plates were prepared from Cellulosepulver MN 300HR at 250 μm (Brinkman Inst.). Plates were developed for 5 hours in the phenol eluant, allowed to dry 24 hours, then developed for 3 hours in the second direction with semi-stench eluant.

Developed plates were sprayed with ninhydrin solution (0.3 g in 100 ml *n*-butanol and 3 ml acetic acid) and placed in a 100 C oven for 3 minutes. Amino-ninhydrin colour complexes were marked and the plates were allowed to cool. Subsequently, plates were sprayed with Hanes reagent (ammonium molybdate-acid solution; see Krebs et al., 81) for the detection of phosphate esters. Amino and phosphate ester colour complexes and their surrounding areas were scraped from the plates. Cellulose powder was analyzed for ^{14}C-activity after shaking and centrifuging according to the method of ^{14}C-glyphosate extraction from plant tissue.

Over 95% of the ^{14}C-activity recovered from each plate corresponded to unaltered ^{14}C-glyphosate.

3.4.2 ^{14}C-picloram

The plant tissue from ^{14}C-picloram treated shoot-root plants was analyzed by extraction whereas whole source-sink plants were analyzed by combustion due to problems with chlorophyll quenching (see Section 3.5).

Frozen tissue from the source-sink plants was loosely wrapped in aluminum foil and freeze-dried in a Virtis Model 10-147 freeze-dryer (Gardiner, New York). Freeze-dried tissue was carefully compressed in a pellet press (Parr Inst. Co., Moline, Illinois). The pellets were placed in combustion boats made from ashless filter paper. Large samples were made into two pellets that were combusted separately. The tissue samples were combusted in a Tri-Carb 306 Sample Oxidizer (Packard Inst. Co., Downers Grove, Illinois) for approximately 1 minute. Carbon-14-labelled CO_2 was trapped and counted in 20 ml of Carbosorb:Permafluor V (12:13) (Packard Inst. Co.).

The efficiency of ^{14}C recovery by the oxidizer was 96.3 ± 0.9% ($s_{\bar{x}}$). Crossover of counts from one sample to the next was less than 2%. In order to minimize crossover, samples of similar ^{14}C-activity were combusted consecutively, with blanks between groups of different amounts of radioactivity.

The plant samples from the shoot-root studies were ground in the Omnimixer or Polytron with 70% ethanol. Ground tissue was shaken for 3 hours and then centrifuged for 30 minutes at 520*g* in graduated centrifuge tubes. Aliquots (1 or 2 ml) of supernatant were added to 15 ml of TEEPP fluor for liquid scintillation counting. The extraction efficiency of ^{14}C-picloram from Canada thistle leaf tissue was 85.0 ± 4.2% ($s_{\bar{x}}$). There was no determination of the ^{14}C-activity remaining in the residue.

3.4.3 ^{14}C-assimilates

Radioactive assimilates produced when plants of Canada thistle photosynthesized in $^{14}CO_2$ were extracted with 70% ethanol. The extraction procedure was identical to that employed for the ^{14}C-picloram treated shoot-root tissue (Section 3.4.2).

The amount of $^{14}CO_2$ photosynthesized by the plants was unknown and therefore no determination of extraction efficiency could be made. MacDonald (93) reported that Canada thistle plant residue that had been treated similarly contained negligible amounts of ^{14}C-activity.

3.5 Liquid Scintillation Spectrometry

All liquid scintillation counting was performed at 15 C in a Searle Isocap 300 liquid scintillation spectrometer (Tracor Analytical Inc., Des Plaines, Illinois). Ethanol extracts of foliage containing chlorophyll, and the red-brown pigments in water extracts of root tissue produced severe quenching (Figure 3 and 4). Chlorophyll quenching from ethanol extracts of plant tissue was too severe for samples to be counted with accuracy. Consequently, ^{14}C-picloram-treated samples from the whole source-sink plant studies were combusted and not extracted. Quenching from leaf and root extracts of the shoot-root studies was minimized by the use of smaller aliquots of supernatant.

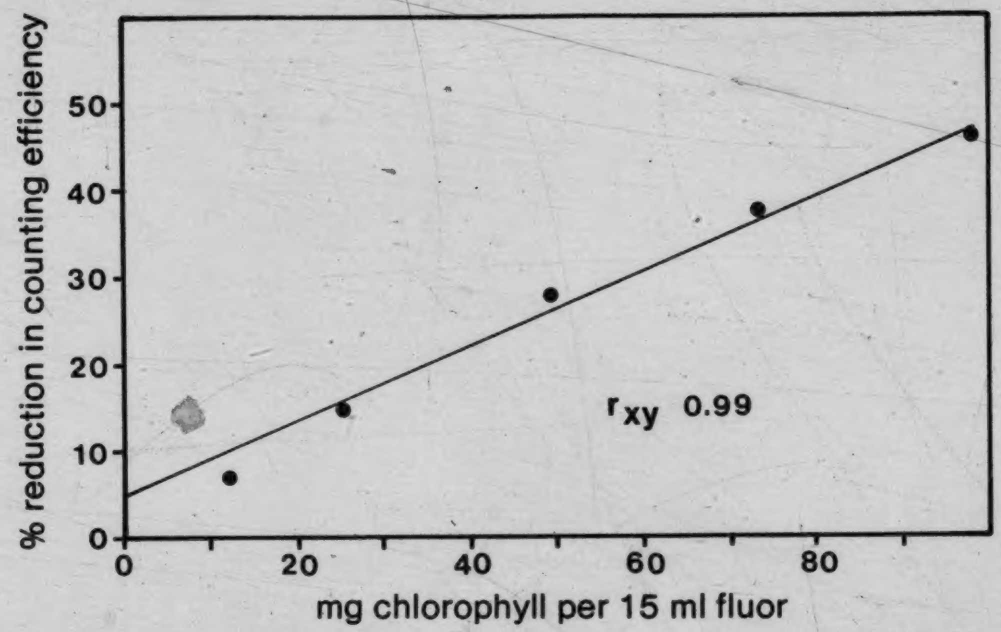

Figure 3. Percentage reduction in liquid scintillation counting efficiency due to chlorophyll quenching

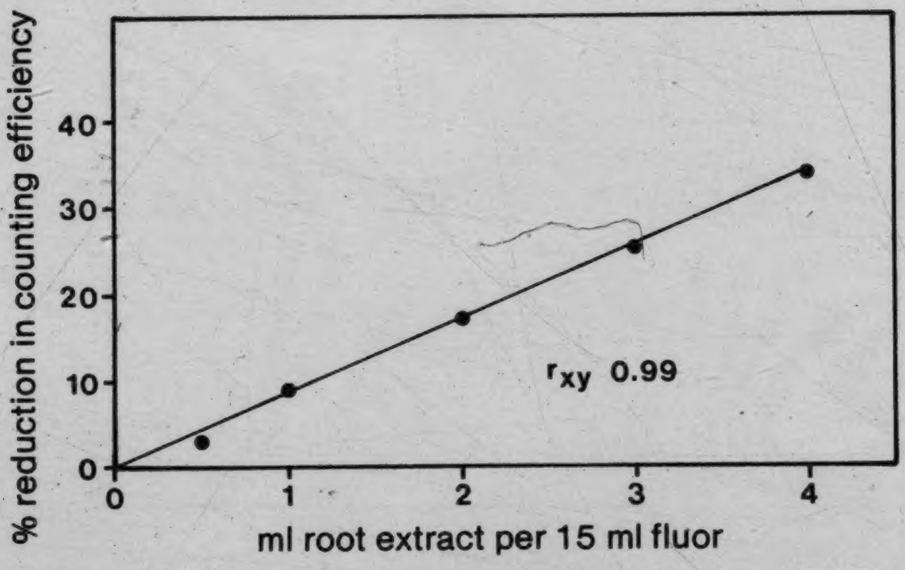

Figure 4. Percentage reduction in liquid scintillation counting efficiency due to quenching from water-extracted Canada thistle root pigments

Quenching was corrected by the sample channels ratio (SCR) for all samples except the combusted ones. For these samples the external standards channel ratio (ESR) was used. Different equations were developed by regression analysis for the correction of quenching in each combination of fluor and solvent (Table 1). The use of SCR and ESR values greater than 1.00 was not accurate for determining absolute activities. Samples with these values were recounted with reduced solvent. No samples were counted until chemiluminescence fell below 5%. Counting was done for 10 minutes or until the standard error of counting reached 0.25%. Counting statistics were not determined.

3.6 Field Experiment

In 1979 a field experiment was initiated at the Ellerslie Research Station to test the effect of ethephon (2-chloroethylphosphonic acid) in combination with glyphosate and dicamba (3,6-dichloro-*o*-anisic acid) for the control of Canada thistle. Four replicates of 6.1 by 3.0 m plots were laid out on a field heavily infested with Canada thistle.

Treatments were applied with a bicycle-type plot sprayer on July 4 and July 18, 1979 when the thistle shoots were 30 cm (early bud) and 90 cm (pre-bloom) high, respectively. Treatments consisted of ethephon, dicamba, glyphosate and combinations of ethephon plus glyphosate or

Table I. Regression lines applied to liquid scintillation count data in order to correct for quenching in four combinations of fluor and solvent

Fluor	Solvent	Regression Line
Permafluor: Carbosorb (12:13)	none	P=110.0 - 87.1(ESR)
Aquasol	water	P=89.8 - 50.6(SCR)
Toluene: 2-ethoxyethanol: PPO:POPOP(TEEPP) 670:330:4:0.5, v/v/w/w)	ethanol	P=85.4 - 40.0(SCR)
TEEPP	benzene	P=89.1 - 47.2(SCR)

P = percent efficiency
SCR = samples channels ratio
ESR = external standards channel ratio
PPO = 2,5-diphenyloxazole
POPOP = 1,4-bis-2-(5-phenoxyloxazolyl)-benzene

dicamba. The combinations were applied as a tank-mix or the ethephon was applied 14 days prior to the herbicide treatments. Details of the treatments and treatment rates are recorded under Section 4.10.

To eliminate early annual weeds, the whole trial was oversprayed with 2 kg ai/ha paraquat (1,1'-dimethyl-4,4'-bipyridinium ion) on May 3, 1980. Due to the heavy Canada thistle infestation in some plots, the whole trial was oversprayed with 2.2 kg ai/ha glyphosate on July 6, 1980. Thistle counts were taken on September 22, 1979, June 30, 1980 and May 30, 1981 ($2m^2$ quadrants counted per plot).

3.7 Statistical Analysis

Experiment 3.3.1.1 (Absorption and translocation of ^{14}C-glyphosate and ^{14}C-picloram from basal and apical leaves) and Experiment 3.3.3 (Retention of herbicide by lanolin rings) were initially arranged with five replicates. The herbicides were applied on different days and, therefore, in order to compare the results from each of the herbicide treatments, the experiments were analyzed as completely randomized experiments with 10 and 5 repeats for Experiments 3.3.1.1 and 3.3.3, respectively.

In Experiment 3.3.2.3 (Effect of shoot size on herbicide translocation into root tissue) the rates of glyphosate and picloram differed. In order to compare the translocation of these two herbicides, data were adjusted by using the total amount of herbicide recovered as a concomitant variable. Data were further adjusted to correct for negative values (151).

For Experiment 3.3.1.5 (Translocation of non-radioactive chemicals past a petiole girdle) the number of leaves in the apex prior to herbicide treatement was used as the concomitant variable in performing an analysis of covariance and in adjusting the treatment means.

The remaining experiments, including Experiments 3.3.2.3 and 3.3.1.5, were analyzed as randomized block experiments. Deviation lines on all graphs and all plus-minus values in tables refer to standard errors of the means.

4. RESULTS AND DISCUSSION

4.1 The Absorption and Translocation of ^{14}C-glyphosate and ^{14}C-picloram from Basal and Apical Leaves

The total recovery of ^{14}C-picloram and ^{14}C-glyphosate from plants treated on the apical or basal leaves varied according to the place of application, the herbicide applied and the number of days after treatment that the plants were analyzed. Up to 36% of the ^{14}C-glyphosate applied to the apex was not recovered (Table II). Comparatively, only 10% of the ^{14}C-picloram was not recovered. After basal leaf application, 39% of the ^{14}C-glyphosate and 23% of the ^{14}C-picloram was not recovered. Although differences in recovery are evident from Table II (especially the lower recovery of glyphosate compared to picloram) only the interaction between day and herbicide was significant (p=0.01). This probably reflects the lower recovery of glyphosate on day 7 as well as a lower recovery of picloram on days 1 and 3 for which there is no explanation. Furthermore, the effect of using different methods for detecting ^{14}C-activity, on the amounts recovered cannot be overlooked.

The loss of ^{14}C-herbicide following basal leaf application could be due to the translocation of herbicide to the unanalyzed roots. Results of Devine (38) indicate that as much as 20% of the applied glyphosate can be translocated to the roots of Canada thistle. Roots were not analyzed for radioactivity in this study and therefore they

Table II. Total radioactivity (as % of applied dose) recovered from source-sink plant systems following ^{14}C-picloram or ^{14}C-glyphosate treatment to the apical or basal leaf. Expt. 3.3.1.1

	APPLICATION POINT						
Days after trtmt.	Apical		Basal		Average of Apical + Basal		
	Pic	Gly	Pic	Gly	Pic	Gly	Diff.
1	85.5	64.2	72.4	63.2	79.0	63.7	15.3
3	83.3	67.4	69.5	65.5	76.4	66.5	9.9
7	100.8	61.3	87.8	54.4	94.3	57.9	36.4
Average of 3 Harvest Dates	89.9	64.3	76.6	61.1	83.2	62.7	20.5

* LSD 0.05 for H x D interaction is 17.5

could be a source of radioactivity loss.

Translocation of ^{14}C-activity to the roots cannot account for the ^{14}C-activity lost after apical application since very little activity was translocated basipetally after ^{14}C-herbicide treatment of the apex. Many theories have been proposed in order to explain losses of ^{14}C-glyphosate in similar studies. Sandberg et al. (128) reported that up to 50% of the ^{14}C-glyphosate applied to excised leaves had disappeared within 25 days. It has been suggested that microbes on the leaves of treated plants may be degrading ^{14}C-glyphosate to $^{14}CO_2$ or a volatile metabolite (128,169). Studies by Schultz and Burnside (131) have shown that less than 0.5% of the applied ^{14}C-glyphosate was recovered in sodium hydroxide and ethylene glycol traps. They were able to account for all the ^{14}C-activity applied to the plants and concluded that the amount of ^{14}C-glyphosate lost to $^{14}CO_2$ was negligible.

Loss of labelled glyphosate as $^{14}CO_2$ could be species or environment specific. Schultz and Burnside (131) also reported no recovery of $^{14}CO_2$ from ^{14}C-2,4-D [(2,4-dichlorophenoxy)acetic acid] treated hemp dogbane. This is contrary to reports using bean where over 17% of the ^{14}C-labelled 2,4-D was recovered as $^{14}CO_2$ (161).

The loss of labelled herbicide by root exudation has also been suggested. Schultz and Burnside (131) found up to 15% of the applied ^{14}C-glyphosate to be exuded from the roots of hemp dogbane, 12 days after treatment. This is contrary to other reports of less than 3% root exudation (31,38,57). The large quantity of exuded ^{14}C-glyphosate reported by Schultz and Burnside could be an artifact of the hydroponics system they employed.

It is worthy of note that ^{14}C-picloram losses in plant studies have not been substantial (139). This is probably due to the resistance of picloram to microbe and plant degradation.

The amount of ^{14}C-glyphosate and ^{14}C-picloram recovered in the washes of herbicide-treated basal and apical leaves significantly decreased over time (Figure 5). Most of this decrease was after the first day following treatment with little or no difference in the amount of herbicide detected in the leaf washes between days 3 and 7.

The wash from the treated leaves of the apex contained considerably less radioactive picloram than the basal leaf wash. There was no difference in the amount of radioactivity recovered in the wash of the apex or basal leaves treated with glyphosate.

The amount of ^{14}C-glyphosate extracted from the apical leaves 1 day after treatment was 38% of the total applied (Figure 6). In contrast, 80% of the picloram was found in the apex after the first day. Over the next 6 days, the average radioactivity found in the ^{14}C-glyphosate-treated apical leaves increased by only 6% compared to 19% for picloram. Picloram appeared to be taken up by the basal leaves continually even after 7 days (Figure 7). For glyphosate the ^{14}C-activity found in the treated leaf decreased after day 1, although this decrease was not significant. A decrease in the amount of ^{14}C-herbicide found in treated basal leaves would be expected as the herbicide is translocated to the apex and stem tissues.

The absorption of herbicide by leaves has been measured either by the amount of radioactivity remaining on treated leaves and recovered in solvent washes of the treated leaf surface (radioactivity not taken up by the leaf) or by the total amount of radioactivity found in the plant. Since the

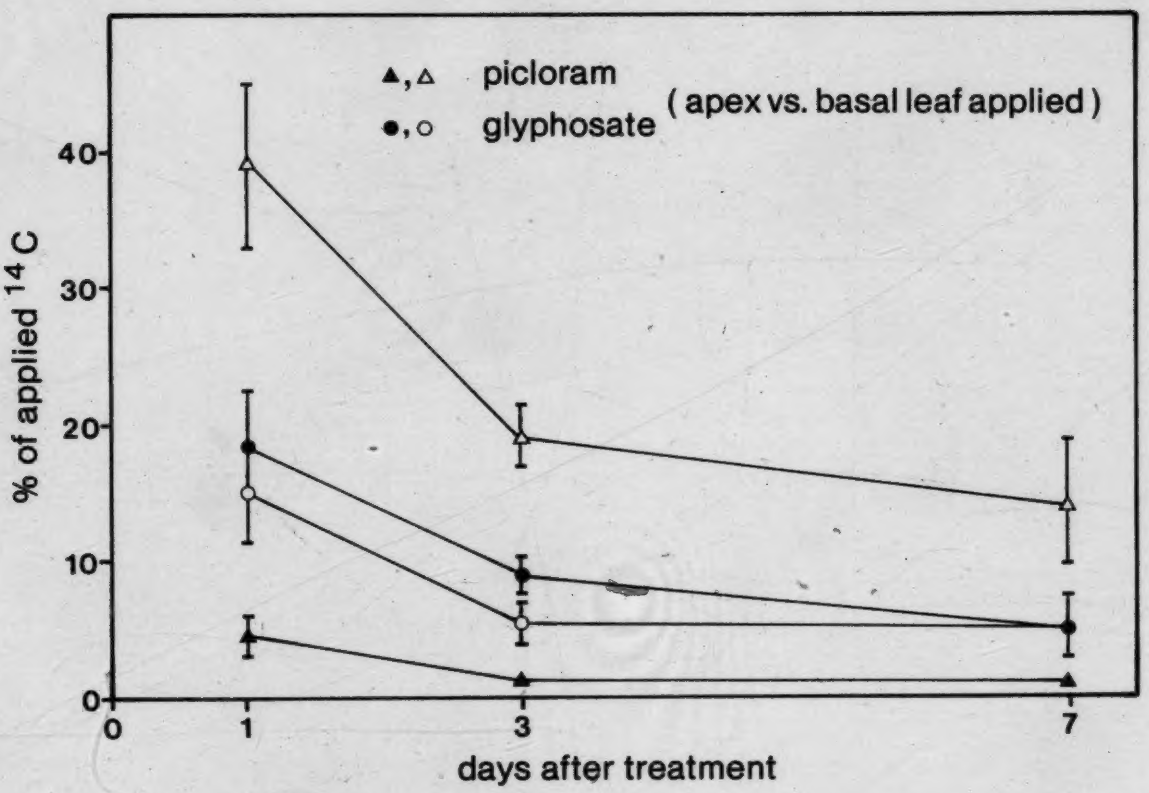

Figure 5. Recovery of ^{14}C-activity from leaf washes following apical and basal leaf ^{14}C-herbicide treatments. Expt. 3.3.1.1

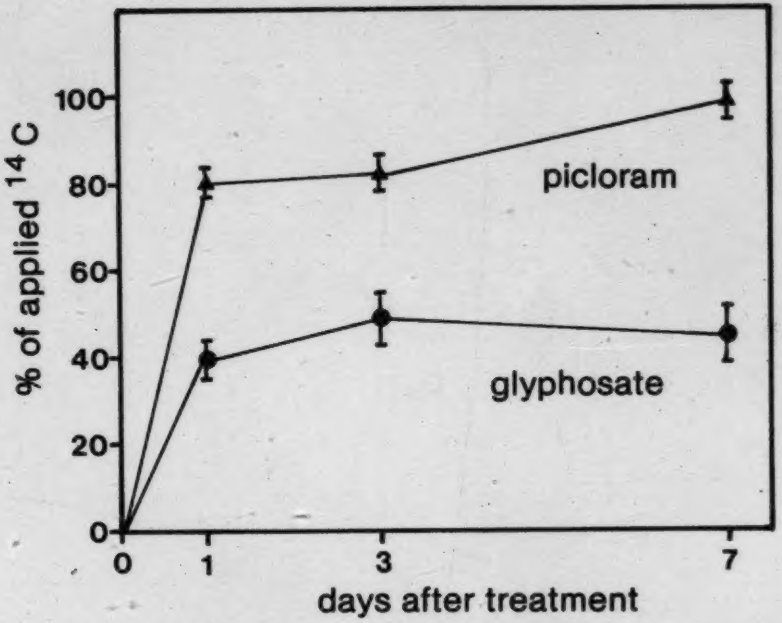

Figure 6. Recovery of ^{14}C-activity from ^{14}C-herbicide treated apical leaves. Expt. 3.3.1.1

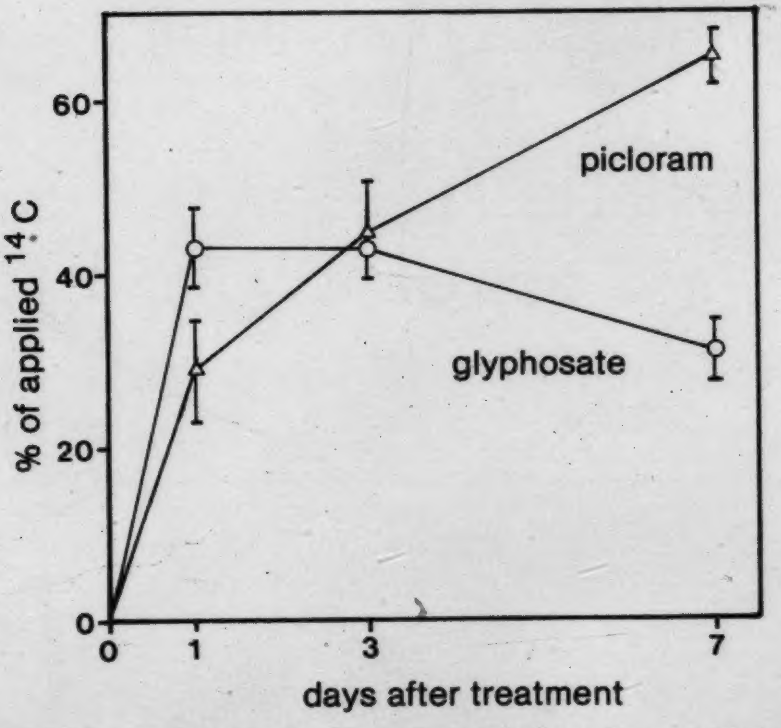

Figure 7. Recovery of ^{14}C-activity from ^{14}C-herbicide treated basal leaves. Expt. 3.3.1.1

translocation of herbicide to the roots was not monitored, there are no data representing total ^{14}C-herbicide taken up by basal leaves. Data for ^{14}C-herbicide taken up by apical leaves are available since there was no translocation of herbicides from the apical leaves into the roots (reported in Section 4.2). For the apical leaf treatments the absorption of herbicides from the apical leaves as measured by the disappearance of radioactivity from the leaf washes (Figure 5) or by increases in radioactivity in the plants (total derived from Figures 6 and 7) is similar. Substantial increases in radioactivity recovered in the plants after 1 day correspond to substantial decreases in radioactivity recovered from apical leaf washes.

In the following discussion the leaf wash data will be regarded as a measure of herbicide absorption by the leaf. The difference in the amount of ^{14}C-picloram remaining on the basal leaves compared to the apical leaves has already been mentioned. If the higher disappearance of ^{14}C-picloram from apical leaf washes is attributable only to leaf absorption and not to gaseous or microbial losses, then it appears that the age of the treated leaf plays a significant role in the amount of picloram absorbed. In contrast, there was no difference in the uptake of glyphosate by the young apical or mature basal leaves.

Owing to less epicuticular waxes the cuticle of younger tissue will offer less resistance to herbicide uptake. Earlier studies (131,137) have shown that leaf age is a factor for the uptake of picloram and glyphosate. Schultz and Burnside (131) found a significant difference in the amount of ^{14}C-glyphosate absorbed by young and mature leaves. A lack of a similar difference in this study may be due to the use of a different species and the use of different surfactants in the treatment solutions. A number of surfactants are required in order that a lethal quantity of the polar molecule of glyphosate is taken up by the treated leaves (167). A change in the types and combinations of these surfactants has resulted in significant changes in the leaf absorption of glyphosate (167).

The lack of apparent glyphosate absorption by leaves after 3 days is in agreement with the results of other researchers (28,38,131). The degree of picloram absorption by leaves in this study is also comparable to that in other studies. For Canada thistle and huisache, picloram absorption by treated leaves had become negligible only after 10 days (17,139).

Concerning leaf absorption of herbicides, it should be noted that leaves became necrotic between 3 and 5 days following treatment with ^{14}C-glyphosate. This could explain the lack of glyphosate absorption after 3 days. Leaves treated with picloram became chlorotic and only slightly necrotic within 7 days.

After application to a basal leaf, ^{14}C-glyphosate and ^{14}C-picloram were readily translocated out of the leaf to the stem and apex. The amount of glyphosate in the stem reached a maximum by day 3 and declined thereafter (Figure 8). This decline was probably due to the continued translocation of glyphosate to the plant apex. The decline in ^{14}C-activity recovered from the stem supports the theory that glyphosate is not bound to vascular plant tissue in significant quantities.

Even though picloram uptake by the treated leaf continued until day 7, the accumulation of ^{14}C-picloram in the stem had peaked on day 1 (Figure 8). Picloram did not attain levels greater than 2,000 dpm/g of fresh stem tissue (1% of applied dose). Glyphosate reached a significantly higher level of 4,000 dpm/g of fresh tissue at 3 days. It should be noted that ^{14}C-picloram quantities in the stem did not change significantly, decrease or increase, over time. Bovey et al. (17) have reported that picloram accumulated in the stem of huisache. This retention may indicate that picloram has become bound to cell tissue and cannot be remobilized.

The amount of glyphosate reaching the apical leaves after a basal leaf treatment was significantly more than the corresponding amount of picloram (Figure 9). Glyphosate accumulated in the apex to the extent of 15% of the applied dose. In comparison, a maximum of only 4% of the applied picloram was recovered from the apex. After 3 days there was no significant change in the total amount of ^{14}C-activity found in the apex of plants treated with glyphosate or picloram.

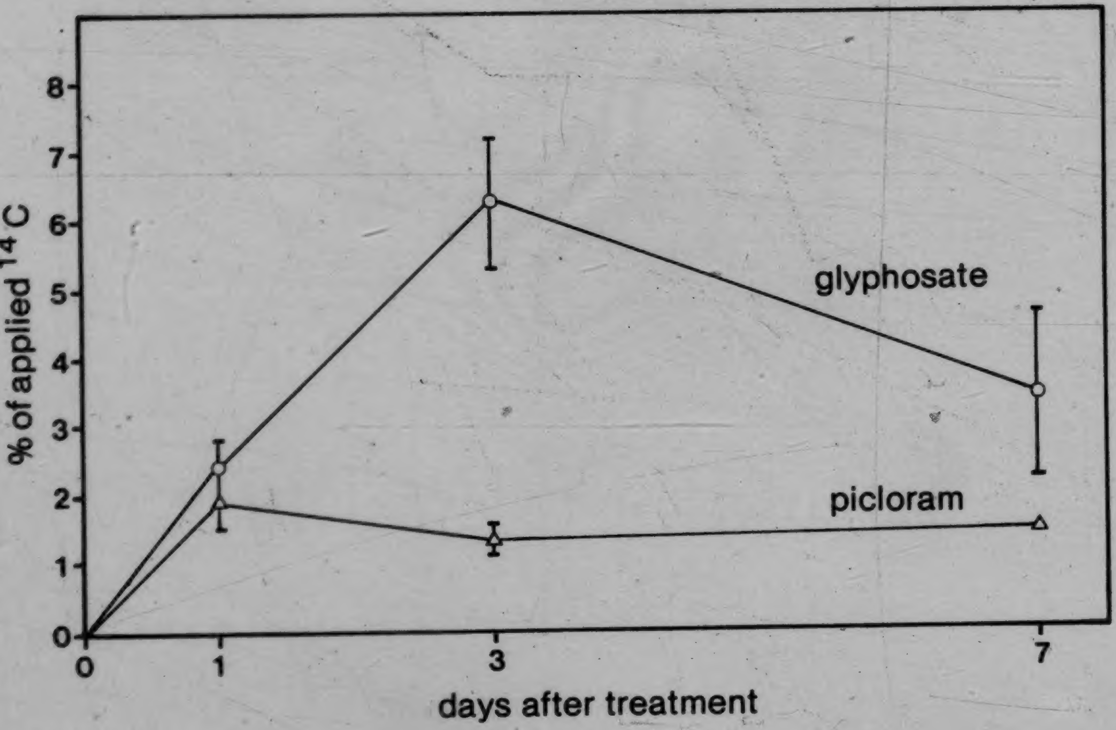

Figure 8. Recovery of ''C-activity from stems following ''C-herbicide treatments to a basal leaf. Expt. 3.3.1.1

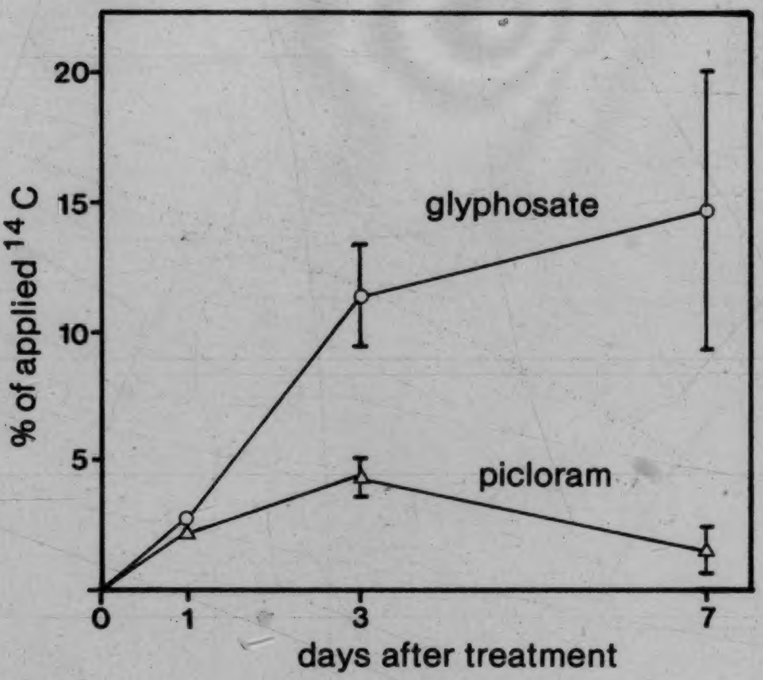

Figure 9. Recovery of ¹⁴C-activity from apices following ¹⁴C-herbicide treatments to a basal leaf. Expt. 3.3.1.1

When expressed as dpm/g of fresh tissue, the ^{14}C-activity in the apex after glyphosate treatment of the basal leaf was not significantly different over the 3 times of harvest although the difference between between the two herbicides was significant (Figure 10). The difference in total amount of ^{14}C-activity recovered from the apices was significant over different times of harvest and between the two herbicides (Figure 9). This loss in significance when the data is expressed as dpm/g as compared to total ^{14}C-activity is attributed in part to the variability in the fresh weights of the plant tissues.

From the plants in Experiment 3.3.1.1 it was noted that the amount of ^{14}C-picloram which did reach the apex of basal leaf treated plants did not cause any observable herbicidal affects to the apical leaves. In comparison, herbicidal activity in the form of chlorosis and necrosis of the leaves were present in the apex 3 days after the basal leaf had been treated with glyphosate.

This experiment suggests that glyphosate is more mobile and accumulates in the apex to a greater extent than picloram. Although picloram was able to reach the apical leaves it appears that the amount able to reach these leaves from a basal leaf is limited. Picloram has been found to limit the translocation of assimilates (86,138) and may be limiting its own translocation in this study. The reported ability of picloram to cause phloem disruption leads one to

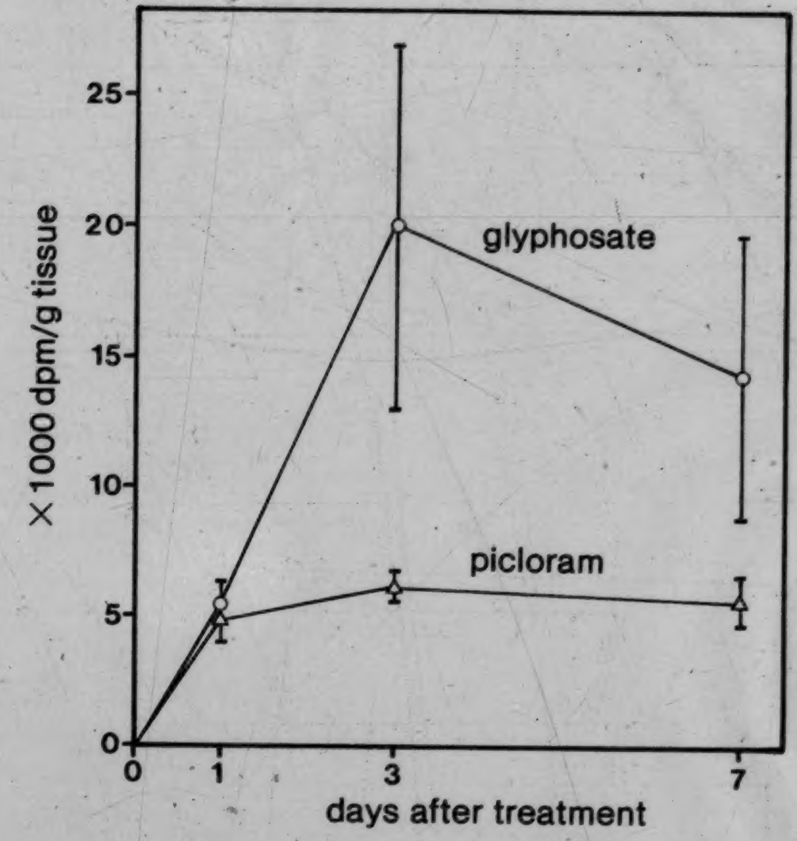

Figure 10. Dpm/gram of fresh apical leaves following a ^{14}C-herbicide treatment of the basal leaf. Expt. 3.3.1.1

hypothesize that the reduced translocation of picloram in the phloem to the apex was due to phloem destruction by the herbicide itself.

4.2 Basipetal Transport from the Apex

From Experiment 3.3.1.1 it was found that significantly more glyphosate than picloram was translocated into the stem and basal leaf below an apex treated with herbicide (Figure 11). Of the applied glyphosate, 10% was found in the stem tissue. This was signicantly more than the 0.5% of applied picloram found in the stem.

In Experiment 3.3.1.2 the stem intervening the apex and basal leaf was partitioned into three sections and therefore the extent to which ^{14}C-herbicide moved down the stem could be quantified. Except for the first stem section, the amounts of herbicide in the stem sections and the basal leaf were low (0.2% of applied dose for glyphosate, Table III). The total amounts translocated into the stem were similar to those found in Experiment 3.3.1.1 (Figure 11). In this study, 10.7% and 0.7% of the applied glyphosate and picloram, respectively, were found in the stem sections and basal leaf.

The only significant difference in distribution of radioactivity between the two herbicides was the greater amount of glyphosate compared to the amount of picloram found in the first stem section and the basal leaf. For the

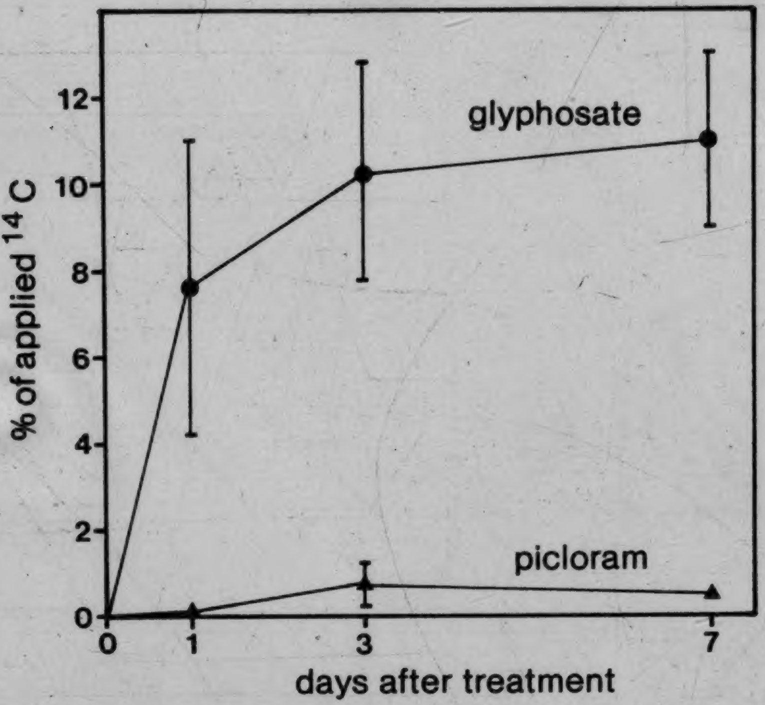

Figure 11. Recovery of ^{14}C-activity from the stem intervening a ^{14}C-herbicide treated apex and a basal leaf. Expt. 3.3.1.1

Table III. Recovery of ^{14}C-activity from stems and basal leaves following ^{14}C-herbicide treatment of apical leaves. Expt. 3.3.1.2

Means (%of applied dose)

	Glyphosate		Picloram		
Apex	363572	(81.8)	454793	(102.4)	
Stem-1	45110	(10.2)	2543	(0.6)	*
Stem-2	734	(0.2)	164	(0.0)	
Stem-3	930	(0.2)	208	(0.0)	
Basal leaf	743	(0.2)	97	(0.0)	*
Total recovered	411089	(92.6)	457775	(103.1)	

* significant difference between herbicide treatments at the 5% level

other two stem sections the plants treated with glyphosate appeared to contain more ^{14}C-activity than the corresponding plants treated with picloram but these differences were not significant.

One explanation for the movement of glyphosate down a stem could be that the treated apical leaves may have begun to export photosynthate. Glyphosate is slow to disrupt plant biochemical activity and plant structures, especially those involved with photosynthesis (20,123). Therefore, apical tissue would be capable of exporting photosynthate. Although these assimilates will be translocated predominantly to the younger apical leaves, no doubt some will be translocated basipetally. This theory for basipetal movement does not explain why ^{14}C-glyphosate was found in significant quantities in only the first stem section. An alternative hypothesis is that glyphosate is mobile in the stem in a direction opposite to the transpiration stream, even when assimilate transport is low.

4.3 The Translocation of ^{14}C-assimilates from a Basal Leaf Exposed to $^{14}CO_2$

A substantial amount of ^{14}C-activity was recovered in the apex of plants in which a basal leaf was exposed to $^{14}CO_2$ (Table IV). This indicates that acropetal translocation of assimilates was great in these plants. In addition, the presence of ^{14}C-activity in the lower stem indicates that assimilates were able to move basipetally from the

Table IV. Distribution of ^{14}C-activity in Canada thistle following exposure of a mature leaf to $^{14}CO_2$ (x1000 dpm). Expt. 3.3.1.3

Days	Apex	Upper Stem	Lower Stem	Exposed Leaf
1	688±84*	305±146	185±58	633±246
3	280±159	94±35	62±15	661±142
7	466±141	98±46	49±22	410±170
Avg.	478±84	165±55	98±26	568±96

* means ± standard error of the mean of 5 repeats

basal leaf. Due to the unknown and variable amount of $^{14}CO_2$ available to and assimilated by each plant, these results are qualitative only. No conclusions about differences in translocation over time can be drawn due to the variation in individual plant photosynthetic and translocation rates. Plant to plant variability due to different photosynthetic and translocation rates can also explain a great deal of the variability found in Experiment 3.3.1.1 for the whole plant source-sink systems treated with herbicide.

4.4 The Effect of Girdling on Acropetal and Basipetal Translocation

Steam girdling the stem below the basal leaf did not change the distribution pattern of ^{14}C-picloram after apical application (Table V). After application of ^{14}C-picloram to the basal leaf and similar girdling, it appeared that the amount of ^{14}C-picloram in the apex had increased (Table VI). An analysis of variance indicated that this increase was not

Table V. The effect of steam-girdling the stem below a basal leaf on the recovery of ^{14}C-activity from source-sink plant systems 3 days following ^{14}C-picloram treatment of the apical leaves. Expt. 3.3.1.4

	Plant part	Girdled	Non-girdled
Total dpm	Apex	350332	394504
	Stem	833	280
	Leaf	573	35
	Wash	2203	2937
Dpm/ gram	Apex	327705	161138
	Stem	277	64
	Leaf	726	16

Table VI. The effect of steam-girdling the stem below the basal leaf on the recovery of ^{14}C-activity from source-sink plant systems 3 days after ^{14}C-picloram treatment of the basal leaf. Expt. 3.3.1.4

	Plant part	Girdled	Non-girdled
Total dpm	Apex	17048	16505
	Stem	6124	4389
	Leaf	157720	54076
	Wash	99191	30576
Dpm/ gram	Apex	12429	6989
	Stem	2534	1081
	Leaf	150694	57897

statistically significant (*p*=0.05).

Stem girdling will prevent basipetal translocation to the root sink. An increase in the pool of herbicide available for translocation to the apex should result, and theoretically there would be an increase in the translocation of herbicide to the apical leaves. From this experiment it was not possible to detect any changes in the amount of picloram reaching the apex, after the root sink had been removed.

4.5 Translocation of Non-radioactive Herbicides Past a Petiole Girdle

Neither picloram nor glyphosate was able to pass a petiole girdle in phytotoxic quantities following application to a basal leaf whose petiole was girdled. This is indicated by the lack of a significant difference in fresh or dry weights of apices from the untreated control plants compared to the apices from herbicide-treated plants with girdled leaf petioles (Table VII). In addition, there was no difference in the number of new leaves formed in the apex between herbicide-treated girdled plants and the untreated controls (Figure 12).

Plants treated with herbicide and with intact petioles were significantly reduced in weight and had a significant reduction in the number of leaves in the apex. In the case of plants treated with glyphosate and picloram, the emergence of new leaves stopped after 5 days. The plants

Table VII. Fresh and dry weights of plant apices, 22 days after herbicide and girdling treatments to the basal leaf. Expt. 3.3.1.5

	Fresh(g)	Dry(g)
Control	31.9	6.1
Girdled control	30.8	5.5
Picloram	0.0	0.0
Picloram girdled	23.6	3.4
Glyphosate	27.5	4.1
Glyphosate girdled	31.0	4.8
LSD 0.5	7.9	1.8

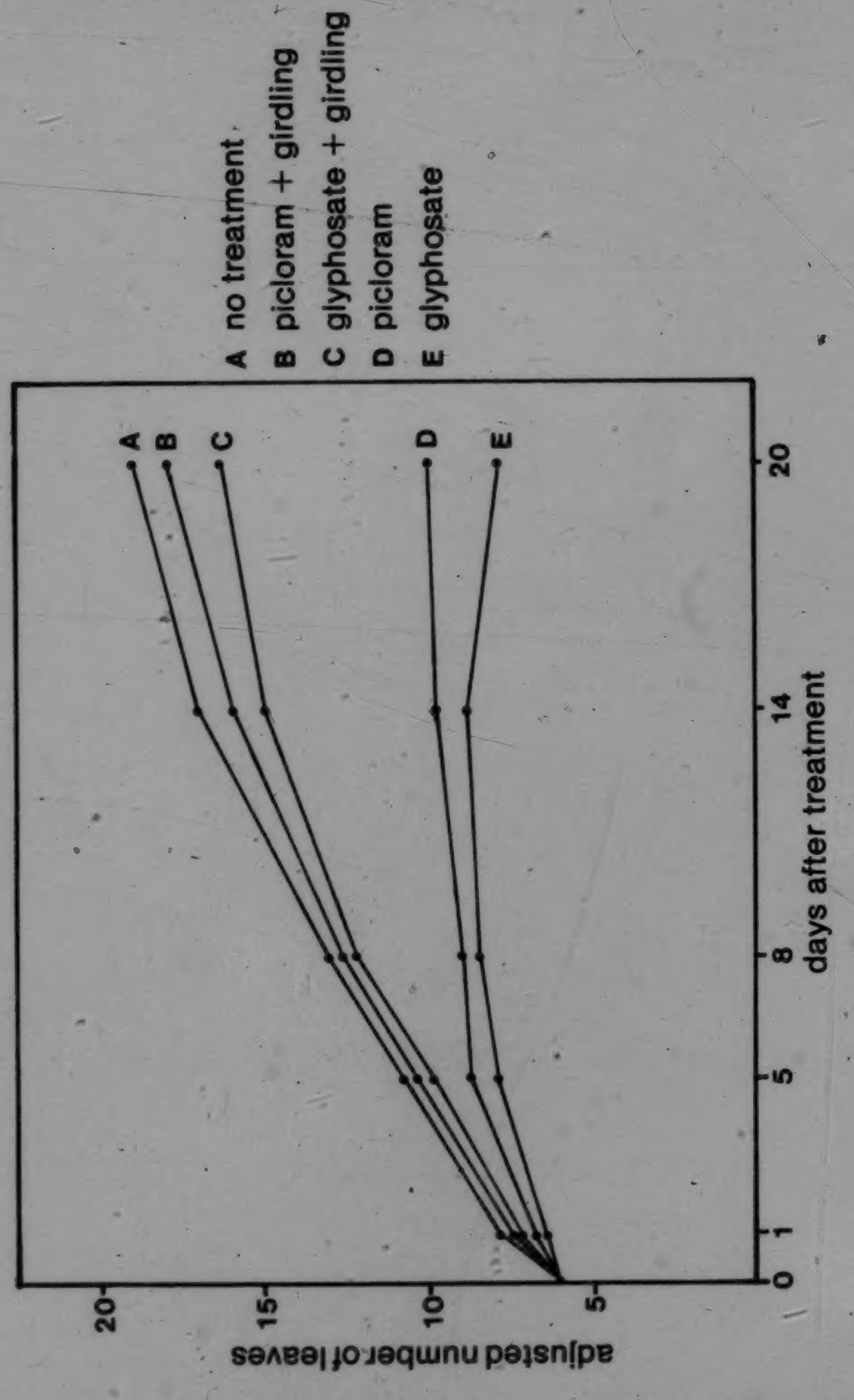

Figure 12. The appearance of new leaves in the apex following herbicide and girdling treatments to the basal leaf. Expt. 3.3.1.5. The number of leaves in the apex prior to herbicide treatment was used as the concomitant variable in adjusting the treatment means.

treated with glyphosate subsequently died and plants treated with picloram became greatly distorted, chlorotic and necrotic.

Had the plants which were girdled and treated with herbicide been affected by the herbicide it would indicate that herbicide was able to by-pass the petiole girdle, probably via the xylem. This experiment was not sensitive enough to detect if small quantities of herbicide were able to by-pass the petiole girdle. It did show that normal herbicide translocation was impeded when phloem tissue was destroyed by girdling.

4.6 Shoot-root Mutilation Studies Involving a Series of Doses of Glyphosate and Picloram

After one day enough glyphosate was translocated from a young shoot treated with a 0.5 mg dose, into the roots to cause the roots subsequently to die and rot (Table VIII). When higher doses were applied to the shoot and/or a longer time period was given in order for the translocation of herbicide to occur from the shoot to the root, the roots also rotted.

In contrast, picloram was not translocated from the treated shoots to the roots in quantities that were able to completely kill the root tissue. Even when herbicide from a 5-mg dose of picloram was allowed to translocate into the root for 3 days, not enough picloram reached the root to kill it completely. In this latter case, 75% of the root

Table VIII. The effect of time required for translocation and herbicide dose on the translocation of a lethal amount of picloram or glyphosate from the shoot to the roots of a shoot-root system. Expt. 3.3.2.1

	Days of Translocation	Herbicide Rate (mg/plant)			
		0.5	1.0	2.0	5.0
Pic	1	++++	++	+	
	3	++	+	+	+
Gly	1	++++	-	-	
	3	-	-	-	+

++++ very healthy with new shoots, equivalent to untreated controls
- dead and rotted root tissue

tissue appeared healthy and a few new roots were evident. This experiment illustrates, quantitatively, the low ability of picloram to move from a young shoot to the root. Glyphosate is very mobile in the same situation.

4.7 Translocation of Shoot-applied Herbicide into Root Tissue

The translocation of ^{14}C-picloram from a young shoot to the adjoining lower stem and root sections was negligible (Table IX). The maximum amount of picloram that was translocated out of the treated shoot was 4390 dpm at hour 2. After 2 hours, the amount of radioactivity recovered from the roots declined until hour 194 when only 50 dpm were found in the lower stem.

Table IX. The total amount of ^{14}C-activity recovered from the root sections and lower stem of a shoot-root system after ^{14}C-picloram treatment of the shoot. Expt. 3.3.2.1

Hours after Treatment	Mean ± $s_{\bar{x}}$
2	4387 ± 1160
6	3360 ± 1525
26	2687 ± 1996
30	468 ± 136
74	302 ± 194
98	1332 ± 690
146	274 ± 123
194	52 ± 52
LSD 0.05	2867

At first, the decrease over time in ^{14}C-picloram recovered from the roots would appear to be due to contamination of the plants harvested in the first 26 hours after treatment. However, there is a steady decrease in recovered ^{14}C-activity between 2 and 26 hours and no ^{14}C-activity was found in the roots after 26 hours (data not reported). These observations suggest that the contamination of the roots was not a problem.

An explanation for these observations could be that ^{14}C-picloram was initially translocated into the roots at a high rate. With time the ^{14}C-picloram could have migrated from the root with the acropetally moving transpiration stream. Gaudiel and Vanden Born (55) have reported that picloram is very mobile in the transpiration stream and is able to transfer from the phloem to the xylem. This transfer to the transpiration stream does not answer why further translocation of ^{14}C-picloram to the roots did not occur. Some reports have noted that picloram will interfere with assimilate translocation (86,138). The disruption of phloem tissue with hormone-induced growth and the subsequent interference of this growth with translocation of herbicide in the phloem is one possible reason for the lack of picloram translocation in this experiment.

The basipetal translocation of ^{14}C-glyphosate out of a treated young shoot into the lower stem and the three root sections of the same plant increased over the first 74 hours (Figure 13). Seventy-four hours after treatment, an average of 18000 dpm of ^{14}C-glyphosate (4.5% of applied dose) could be recovered from the lower stem and root sections. The total translocation of ^{14}C-glyphosate from the shoot did not change significantly after 74 hours.

The accumulation of ^{14}C-glyphosate in the lower stem reached a maximum by hour 30 (3800 dpm, Figure 14). Thereafter, the amount of ^{14}C-glyphosate in the lower stem appeared to decline slightly. The root sections (RT1, RT2, RT3) accumulated ^{14}C-glyphosate up to hour 74 (4600 to 5300 dpm, Figure 15). After hour 74 the amount of ^{14}C-glyphosate in the root tissues became variable, but did not significantly change for any one root section.

The increases in ^{14}C-activity in all tissues between hour 2 and hour 74 were fitted to linear equations by

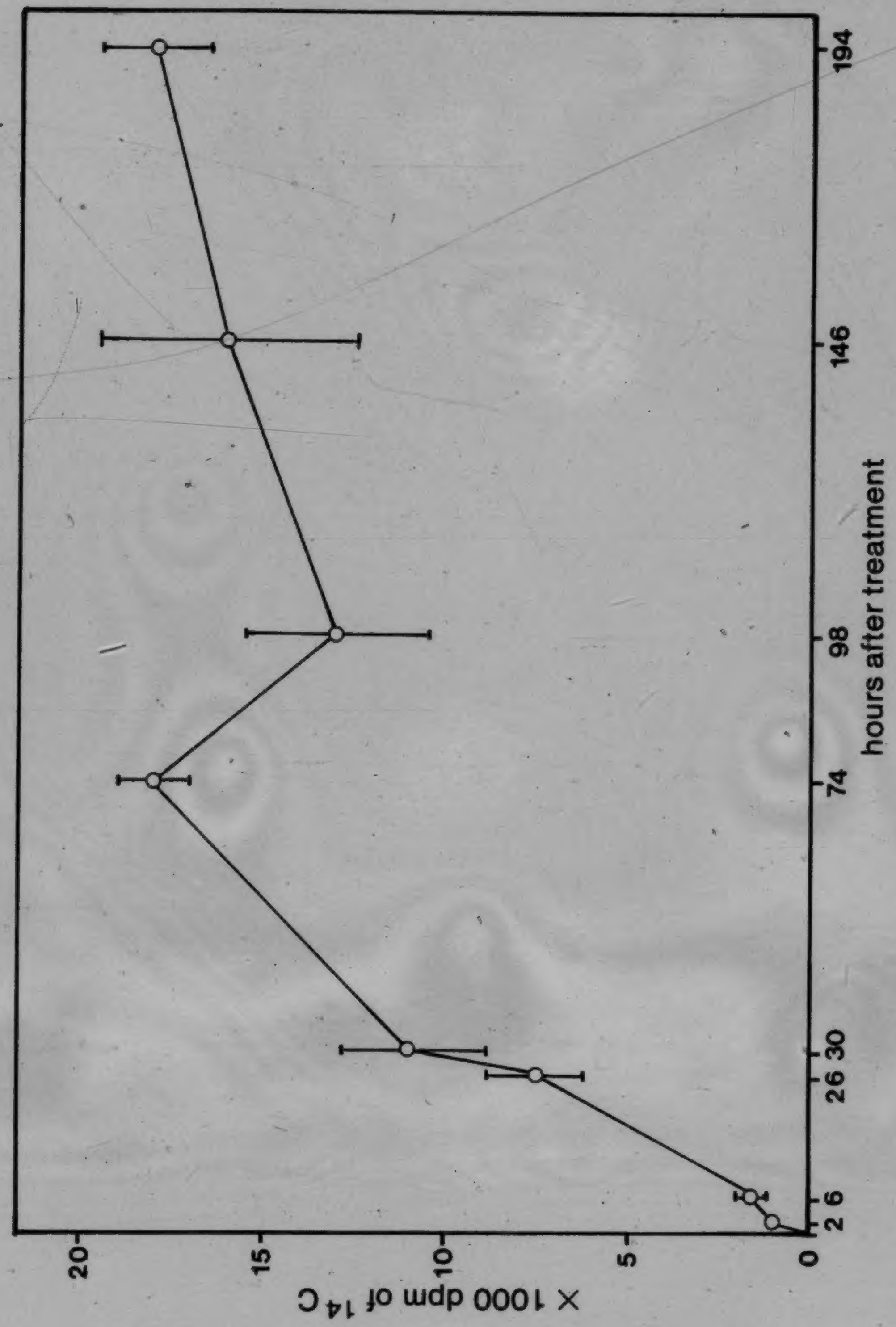

Figure 13. Recovery of ^{14}C-activity, over time, that has been translocated to the root sections and lower stem following treatment of the shoot with ^{14}C-glyphosate. Expt. 3.3.2.2

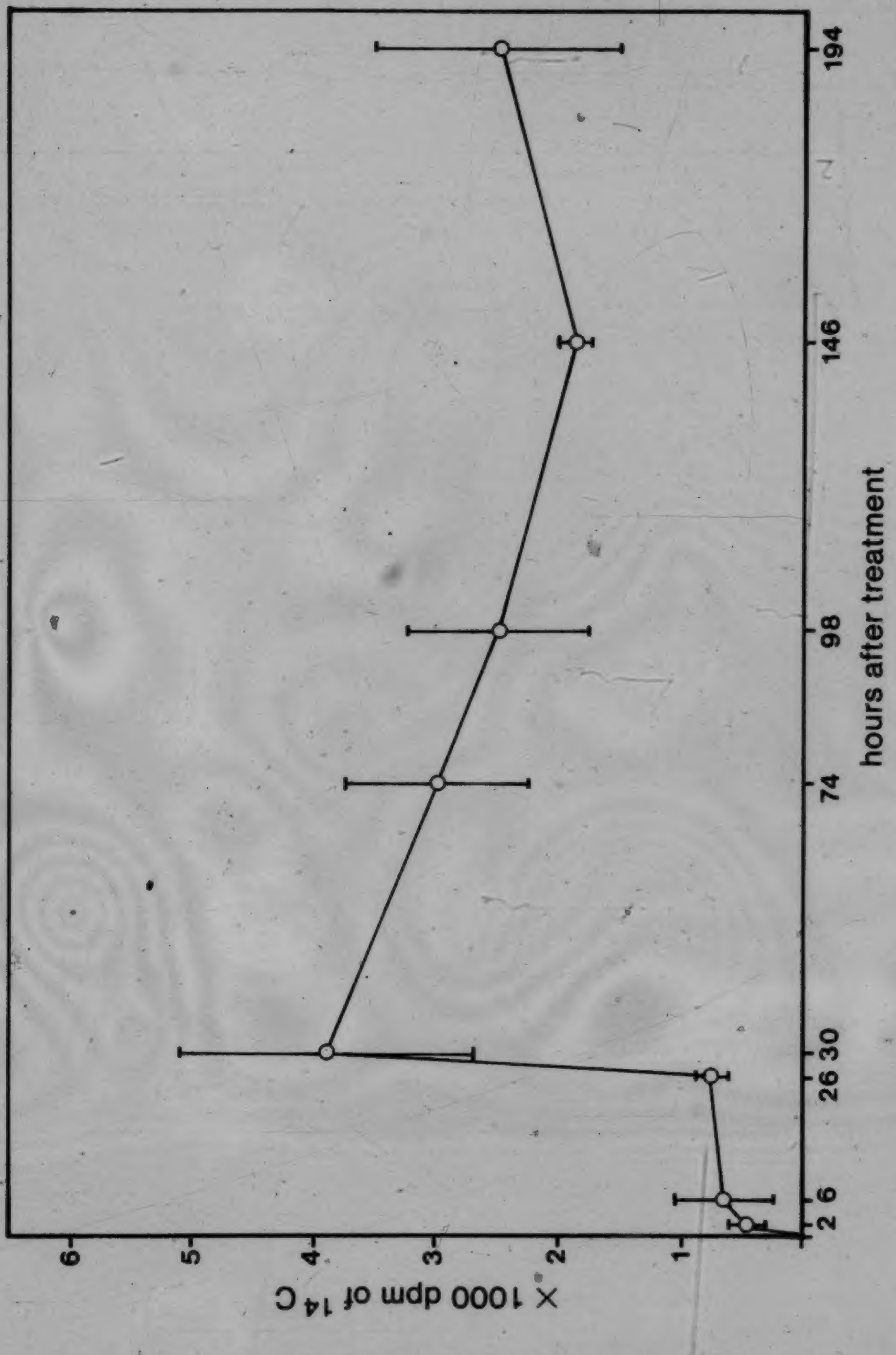

Figure 14. Recovery of ^{14}C-activity from the lower stem, over time , following treatment of the shoot with ^{14}C-glyphosate. Expt. 3.3.2.2

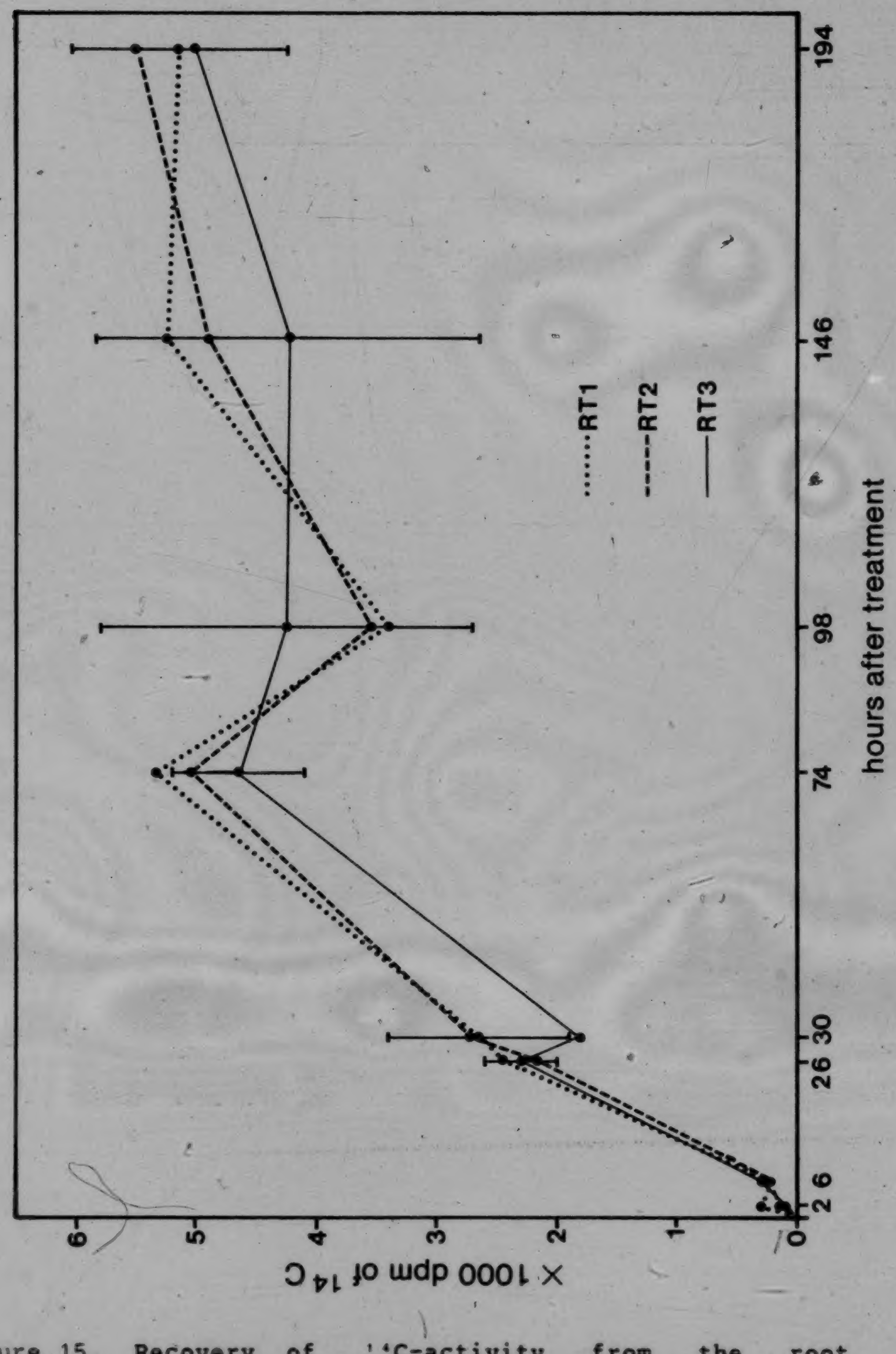

Figure 15. Recovery of ^{14}C-activity from the root sections, over time , following treatment of the shoot with ^{14}C-glyphosate. Expt. 3.3.2.2

regression analysis (Table X). More than 80% of the variation in the data, except in the case of the lower stem tissue, could be explained through these regression lines. In each of the root segments, glyphosate accumulated at approximately 16 ng glyphosate (19 dpm) per hour (Table X).

The ^{14}C-activity remaining in the root tissues after 74 hours was fairly constant at 0.056 mg glyphosate per root segment. This appears to be an equilibrium concentration for glyphosate in the root tissue. No root weights were taken, but by using an estimate of their fresh weight (1.2 g per 6.7 cm root segment), this would be equivalent to 47 ng glyphosate per mg of fresh root tissue. It was not determined whether this concentration of glyphosate was lethal to the root. The concentration of glyphosate recovered from the root tissue was 150 times greater than the concentration of picloram that was lethal to roots of huisache (17).

Compared to glyphosate, picloram was very immobile in the same system. Since the stem tissue did not accumulate ^{14}C-glyphosate to any extent, it would appear that glyphosate does not bind extensively to vascular cells in the stem. The accumulation of ^{14}C-glyphosate in the roots may be attributed to the storage nature of Canada thistle roots. Canada thistle roots are fleshy and possess a great deal of cortex and phloem tissue for carbohydrate storage (63).

Table X. Regression lines for the recovery of ^{14}C-glyphosate between hours 2 and 74 from various sections of a shoot-root system following treatment of the shoot. Expt. 3.3.2.2

Source of ^{14}C	Coefficient of Determination	Regression Line	ng gly accumulated /hr
Stem	0.28	DPM = 42.6(HR)+64	10
RT 1	0.81	DPM = 73.8(HR)+179	17
RT 2	0.81	DPM = 70.2(HR)+123	16
RT 3	0.83	DPM = 66.2(HR)+72	16
Total Trans. from shoot	0.86	DPM = 241.8(HR)+1139	57

4.8 Effect of Shoot Size on Herbicide Translocation into Root Tissue

The amount of ^{14}C-herbicide translocated from the shoots of 1-week (3 to 5 cm high) and 4-week (6 to 13 cm high) old plants to the root sections and lower stem was not significantly different (Figure 16). There was no difference in the quantity of radioactivity found in the tissue at the two times of harvest (days 3 and 9) and, therefore, the data in Figure 16 are pooled over the times of harvest. Only the interaction between shoot size and plant tissue and the three-way interaction of shoot size, herbicide and time were significant (p=0.05). The two-way interaction is the result of more ^{14}C-picloram being recovered from the lower stem and the RT1 and RT2 sections of the larger treated shoots than

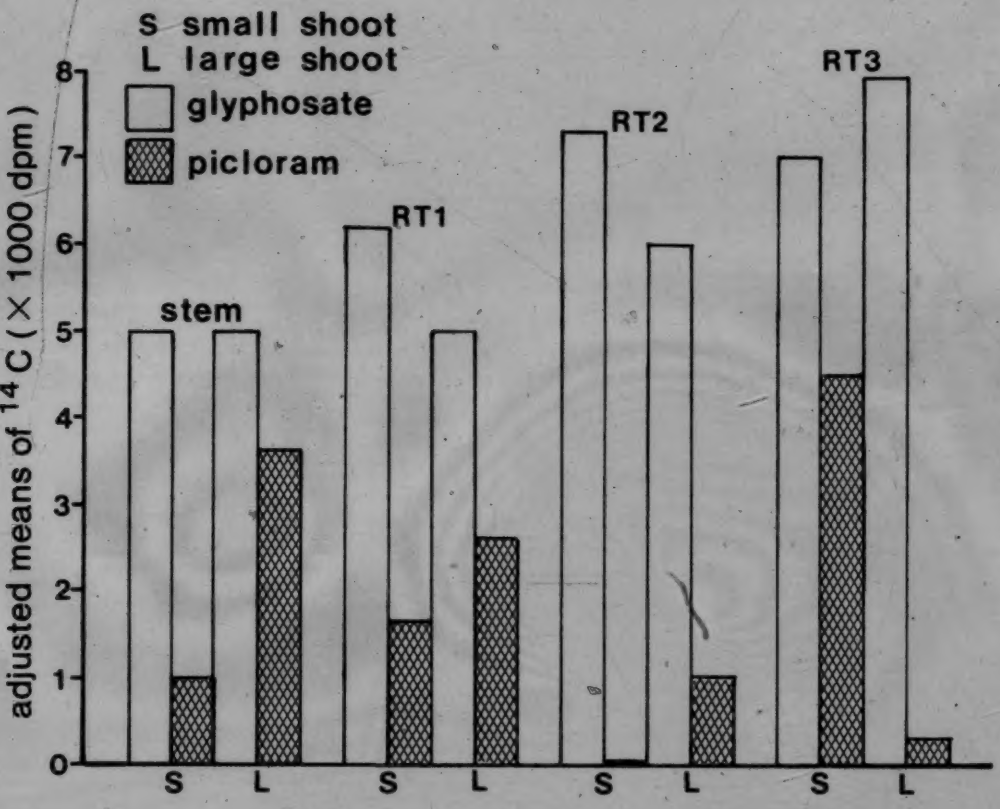

Figure 16. Recovery of ^{14}C-activity translocated to the root sections and lower stem following treatment of various sized shoots with ^{14}C-glyphosate and ^{14}C-picloram. Expt. 3.3.2.3. The total recovered radioactivity was used as the concomitant variable in adjusting treatment means.

from the small shoots, whereas less ^{14}C-picloram was recovered from the RT3 section of the large shoot than from the small shoot. The plant sections of the large and small ^{14}C-glyphosate-treated shoots contained similar amounts of ^{14}C-activity. There is no reasonable explanation as to why ^{14}C-picloram would reach higher levels in the RT3 section of a small plant than a large plant. The higher amount of ^{14}C-picloram found in all the plant sections of the larger plants, except for the RT3 section, may be due to greater translocation of ^{14}C-picloram to the roots from these larger shoots. Although statistical significance has been occluded, probably by plant to plant variability, more ^{14}C-glyphosate than ^{14}C-picloram was recovered from all plant sections (Figure 16). This illustrates again the greater mobility of glyphosate in the vascular system of this plant.

Since the large and small shoots contained a wide range of shoot fresh weights, a correlation between the fresh weight of the above ground foliage and the total amount of ^{14}C-herbicide translocated out of the treated shoot was computed. This correlation was insigificant, r=-0.27 and r=0.24, for glyphosate and picloram treatments, respectively. No definite conclusions could be drawn from this experiment on the effect of the size of the treated shoot on subsequent translocation of herbicide from the shoot to the root.

4.9 Retention of Herbicide by Lanolin Rings

Lanolin rings retained 4.7 ± 0.6% and 1.6 ± 0.4% of the applied ^{14}C-picloram and ^{14}C-glyphosate respectively (Figure 17). With time, the amount of glyphosate found in the lanolin appeared to decrease while the proportion of picloram retained by the lanolin increased slightly. The significantly greater amount of picloram retained by the lanolin could be a result of the more lipophilic properties inherent to picloram. Reported partition coefficients and water solubilites for glyphosate, picloram and other herbicides (Table XI) confirm the lipophilic nature of picloram.

The above results are in disagreement with those of Schultz and Burnside (131), who stated that 90% of the 2,4-D and 57% of the glyphosate applied inside a lanolin ring on a glass slide was retained by the lanolin. Their value for glyphosate retained by lanolin is 36 times greater than that found in this study. Schultz and Burnside did not analyze the lanolin for ^{14}C-activity as was done in this experiment. Instead, they measured the amount of ^{14}C-activity recovered from washes of the lanolin.

Schultz and Burnside (131) also claim that the lanolin reduced the amount of glyphosate and 2,4-D absorbed and subsequently translocated throughout plants of hemp dogbane. The effect of lanolin on the ultimate amount and phytotoxic activity of the herbicides in the plants was not tested in this study. Any such effect is likely to be due to the

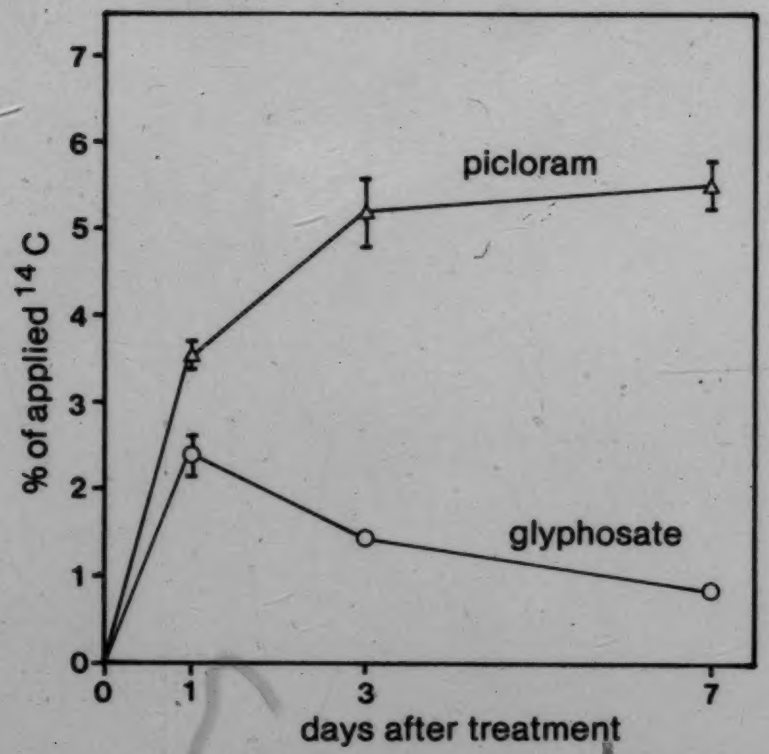

Figure 17. Retention of ^{14}C-herbicide by lanolin rings on leaves of Canada thistle

Table XI. Reported partition coefficients (1-octanol/water) and water solubilities for herbicides.

Herbicide	Partition Coefficient (log P)	Water Solubility ppmw (25 C)
Atrazine	3.7[29]	33[160]
2,4-D acid	2.8[51]	900[160]
Diuron	2.2[29]	42[160]
Glyphosate	-4.0[29]	12000[160]
Picloram acid	-0.9[29]	430[160]

physical presence of lanolin on the leaf. In light of the above results, lanolin is not likely to reduce herbicide phytotoxic activity by withholding the herbicide from leaf absorption.

4.10 Ethephon Treatments in the Field

In the first year after treatment ethephon significantly reduced the number of thistle shoots when it was applied 2 weeks prior to a half rate of glyphosate (Table XII). It did not affect the control of Canada thistle given by dicamba. The presence of ethephon in tank-mixes with glyphosate or dicamba did provide added thistle control. A tank-mix of 2,4-DB [(2,4-dichlorophenoxy)butyric acid] and glyphosate did not add any control to that already obtained by glyphosate alone.

Plants that were treated with ethephon alone became stunted. Their buds appeared burned and most remained closed throughout the season. Although the number of shoots in the plots treated with ethephon was about half that of the untreated control plot in the first fall, by the following summer there was no difference between the ethephon treatment and the weedy control.

The control attained by the dicamba treatment in the first summer was lost by the second summer. All treatments containing glyphosate continued to give good control through 1980.

Table XII. Control of Canada thistle by treatments of ethephon with dicamba or glyphosate in the field, Expt. 3.6

Treatment(kg/ha)	Thistle Counts/m^2		
	Sept.22/79	June 30/80	May 30/81
Ethephon(2.0)	22.8 b	31.3 a	3.2 cd
Glyphosate(1.2)	5.8 c	9.2 bc	12.3 bc
Ethephon + glyphosate (2.0 + 1.2)	7.5 c	10.8 b	21.8 a
Ethephon + glyphosate (2.0 + 1.2) Eth. 2 wks pre gly.	2.8 d	2.0 c	15.0 a
Dicamba(0.6)	11.6 c	28.8 a	0.0 d
Ethephon + dicamba (2.0 +0.6)	20.3 b	24.3 a	3.5 cd
Ethephon + dicamba (2.0 + 0.6) Eth. 2 wks pre dic.	11.1 c	26.4 a	0.8 d
2,4-DB + glyphosate (0.3 +1.2)	6.0 c	9.2 bc	6.2 bcd
Weedy check	41.0 a	32.8 a	4.5 cd

Means in the same column followed by the same letters are not significantly different at the 5 % level using Duncan's multiple range test

The lack of regrowth in the spring of 1981 illustrates the significant effect of the summer 1980 overspray of glyphosate. Those plots that were heavily infested and in the bloom stage at application time had the best results. The original plots treated in 1979 with glyphosate were sparsely infested when sprayed in the summer of 1980. The number of shoots present in these plots increased only moderately between 1980 and 1981.

The dicamba/ethephon tank-mix was reported by Carson and Bandeen (22) to be the most efficient combination on the basis of the amount of herbicide recovered from the roots. This treatment was not very effective in the experiment reported here.

Kossatz and O'Sullivan (79) have reported that tank-mixes of ethephon and amitrole (3-amino-s-triazole), glyphosate or 3,6-dichloropicolinic acid did not improve control over the herbicides used alone. They used a rate of ethephon equal to one quarter of that used in this study. The added control obtained in this study from ethephon may be due to the ability of ethephon to stimulate root bud activity. This enhanced root bud activity may then increase the sink activity and as a result increase general translocation to the roots. Root bud activity was positively affected by ethephon in the greenhouse (24). The translocation of ethephon in tobacco is reported to be apoplastic (41) and, therefore, the ability of ethephon to reach the root buds is questionable.

The added herbicidal effect of ethephon may be due to decreased resistance of the leaf to herbicide absorption as opposed to ethephon increasing root bud activity. Ethephon breaks down to ethylene (100) which can cause senescence of foliage (1,13,105). Senescence involves cell structure reduction and,general tissue disruption (13) which could lead to more favourable circumstances for glyphosate absorption by the plant foliage and subsequent translocation throughout the plant. Carson and Bandeen (22) found increased leaf absorption of 2,4-D and dicamba in the presence of ethephon.

4.11 General Discussion

It was anticipated that the use of the two plant systems reported in this study would reduce the plant-to-plant variability normally associated with perennial plant studies. Variability in the results obtained with the use of the whole plant source-sink system remained great. The source of variability was probably related to the different rates of photosynthesis and translocation characteristic of 6 to 8-week old plants. Variability in the shoot-root system was also evident. The results of the shoot-root system were not severely affected by variability, since there was such a great difference in the translocation phenomena of the two herbicides in it. The advantage of this system was that it required less time to prepare and quenching was not a severe problem when analyzing the plant extracts for radioactivity by liquid scintillation spectrometry. The shoot-root system could be used in future research with various herbicides in order to test the effect of different environmental factors and plant growth regulator treatments on the ultimate transport of herbicides to plant roots.

Glyphosate was notably more mobile than picloram in Canada thistle. The translocation of ^{14}C-glyphosate to the apex of plants from a basal leaf was significantly greater than that for ^{14}C-picloram. Furthermore, glyphosate accumulated in greater quantities in the stem below a herbicide-treated apex, and was translocated basipetally from a young shoot into the attached root system. Transport of the herbicides in the above instances is believed to be predominantly in the phloem. The transport of substances out of a green leaf into the stem is not known to occur in the xylem. The subsequent transport of substances from the stem to the apex may proceed via the xylem or phloem. In addition, the xylem has not been associated with basipetal transport of substances from apical leaves to the lower stem and roots. Therefore, the importance of the phloem to the transport of these herbicides is evident.

The distribution of glyphosate and picloram in plants after application to a basal leaf was similar, but the relative amounts of herbicide transported were different. This was evident from the greater amount of glyphosate than picloram found in the apex. The properties inherent to glyphosate which allow it to translocate in the plant in greater quantities are obscure. These properties are undoubtedly related to the ability of glyphosate to traverse freely across the plasmalemma between the xylem and phloem and may also be related to the relative inability of glyphosate to inhibit its own translocation.

The quantity of picloram found in the roots after treatment of a young shoot was low and decreased with time. Glyphosate accumulated in the roots in quantities which later were able to kill the root tissue. The transport of herbicides to the roots via the symplast is known to occur. But in most reported cases this translocation occurs after the plant has matured when assimilates are being translocated to the roots for winter storage. No report is known which cites the transport of significant amounts of assimilate into the roots from a very young shoot. This lack of basipetal assimilate transport should also pertain to the shoot-root system used in this study.

The fact that glyphosate was translocated to the roots when the roots were not likely acting as sinks for assimilates is a meaningful observation. Glyphosate may be reaching root tissue which is not acting as a strong sink. Controlling all plant tissue capable of plant regeneration is an important step towards excellent control of perennial weeds which possess extensive root systems. Parts of the root which are major sources of regeneration, yet are not strong sinks for assimilates are dormant root buds. The control of root buds with herbicides such as glyphosate would greatly improve perennial weed control.

Further research in search of the chemical properties required for herbicides to be translocated widely in plant tissue would assist in the successful use and development of herbicides in the future. The plant characteristics governing the strength of plant sinks and their ultimate significance to the translocation of assimilates and herbicides in plants also deserve further study.

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APPENDIX : Analysis of Variance Tables

Table A1. Analysis of variance of the recovery of ^{14}C-activity from source-sink plant systems following ^{14}C-herbicide treatment of the apical or basal leaf. Expt. 3.3.1.1

Source	D.F.	Mean Square	F
Application	1	1320	3.37
Herbicide	1	11880	5.85
Time(days)	2	850	0.42
A x H	1	790	1.98
A x T	2	50	0.12
H x T	2	2030	5.08 **
A x H x T	2	40	0.10
Error	105 ‡	390	

** Significant at 1% level

‡ 1 d.f. lost from the error d.f. due to missing value

Table A2. Analysis of variance of the ^{14}C-herbicide recovered in leaf washes of apical and basal leaf treated source-sink plants. Expt. 3.3.1.1

Source	D.F.	Mean Square	F
Application	1	53.53×10^{9}	0.64
Herbicide	1	6.26×10^{9}	0.08
Time(days)	2	37.20×10^{9}	4.58
A x H	1	37.20×10^{9}	10.27
A x T	2	5.46×10^{9}	0.67
H x T	2	0.71×10^{9}	0.09
A x H x T	2	8.12×10^{9}	4.81 **
Error	106 ‡	1.72×10^{9}	

** Significant at 1% level

‡ 2 d.f. lost from the error d.f. due to missing values

Table A3. Analysis of variance of ^{14}C-activity recovered from ^{14}C-herbicide treated apices. Expt. 3.3.1.1

Source	D.F.	Mean Square	F
Herbicide	1	543.23×10^9	138.58 **
Time(days)	2	16.34×10^9	4.16 *
H x T	2	11.46×10^9	2.92
Error	54	3.92×10^9	

* Significant at 5% level
** Significant at 1% level

Table A4. Analysis of variance of the ^{14}C-activity recovered from ^{14}C-herbicide treated basal leaves. Expt. 3.3.1.1

Source	D.F.	Mean Square	F
Herbicide	1	15.21×10^9	0.26
Time(days)	2	30.08×10^9	0.50
H x T	2	59.56×10^9	11.38 **
Error	52 ‡	5.23×10^9	

** Significant at 1% level
‡ 2 d.f. lost from the error d.f. due to missing values

Table A5. Analysis of variance of the ^{14}C-activity recovered from stems following ^{14}C-herbicide treatments to a basal leaf. Expt. 3.3.1.1

Source	D.F.	Mean Square	F
Herbicide	1	20.12×10^9	3.98
Time(days)	2	2.69×10^9	0.53
H x T	2	5.05×10^9	6.59 **
Error	53 ‡	0.75×10^9	

** Significant at 1% level
‡ 1 d.f. lost from the error d.f. due to missing value

Table A6. Analysis of variance of ^{14}C-activity recovered from apices following ^{14}C-herbicide treatment to a basal leaf Expt. 3.3.1.1.

Source	D.F.	Mean Square	F
Herbicide	1	7.20×10^9	6.88 **
Time(days)	2	6.89×10^9	6.59 **
H x T	2	1.53×10^9	1.46
Error	53 ‡	1.05×10^9	

** Significant at 1% level

‡ 1 d.f. lost from the error d.f. due to missing value

Table A7. Analysis of variance of the dpm/gram of fresh apex tissue following ^{14}C-herbicide treatment to a basal leaf. Exp. 3.3.1.1

Source	D.F.	Mean Square	F
Herbicide	1	7.91×10^9	5.37 *
Time(days)	2	3.02×10^9	2.05
H x T	2	2.24×10^9	1.52
Error	53	1.47×10^9	

* Significant at 5% level

Table A8. Analysis of variance of the ^{14}C-activity recovered in various plant tissues (excluding the apex) after a ^{14}C-herbicide treatment to the apex. Expt. 3.3.1.2

Source	D.F.	Mean Square	F
Replicates	4	3.50×10^8	1.13
Herbicide	1	12.38×10^8	1.21
Tissue	3	13.63×10^8	1.24
H x T	3	10.98×10^8	3.80 *
Error	28		

* Significant at 5% level

Table A9. Analysis of variance of the effect of girdling the the stem below a basal leaf on basipetal translocation of ^{14}C-picloram from an apex. Expt 3.3.1.4

Source	D.F.	Mean Square	F
Replicates	4	2.28×10^9	0.07
Girdling	1	1.20×10^9	0.04
Error	34	31.80×10^9	

Table A10. Analysis of variance of the effect of steam girdling the stem below a basal leaf on the recovery of ^{14}C-activity from source-sink plant systems 3 days following ^{14}C-picloram treatment of the apical leaves. Expt. 3.3.1.4

Source	D.F.	Mean Square	F
Replicates	4	0.72×10^9	0.24
Girdling	1	1.08×10^9	0.16
Error	34	44.78×10^9	

Table A11. Analysis of variance of the ^{14}C-glyphosate recovered from the root sections and lower stem of a shoot-root system following treatment of the shoot. Expt. 3.3.2.2

Source	D.F.	Mean Square	F
Replicates	3	4.31×10^6	2.15
Time	7	48.18×10^6	24.01 **
Root tissue	3	9.11×10^6	4.54 **
T x R	21	2.86×10^6	1.42
Error	93	2.01×10^6	

** Significant at 1% level

Table A12. Analysis of variance of the ^{14}C-glyphosate recovered from the root tissue sections of a shoot-root system following treatment of the shoot. Expt. 3.3.2.2

Source	D.F.	Mean Square	F
Replicates	3	2.06×10^6	0.99
Root tissue	2	0.73×10^6	0.35
Time(days)	7	49.72×10^6	23.97 **
R x T	14	0.45×10^6	0.22
Error	69	2.07×10^6	

** Significant at 1% level

Table A13. Analysis of variance of the total ^{14}C-picloram recovered from a shoot-root system after treatment of the shoot. Expt. 3.3.2.2

Source	D.F.	Mean Square	F
Replicates	3	1.44×10^9	0.31
Time(days)	7	2.20×10^9	0.48
Error	21	4.61×10^9	

Table A14. Analysis of variance of the total ^{14}C-glyphosate recovered from a shoot-root system after treatment of the shoot. Expt. 3.3.2.2

Source	D.F.	Mean Square	F
Replicates	3	2.13×10^8	0.34
Time(days)	7	7.44×10^8	1.19
Error	21	6.25×10^8	

Table A15. Analysis of variance of values for ^{14}C-herbicide recovered from root sections of different sized shoot-root systems following treatment to the shoot (excluding the treated shoot). Expt. 3.3.2.3. Values were adjusted by covariance using the total recovered radioactivity as the concomitant variable.

Source	D.F.	Mean Square	F
Replicates	3	3.68x10^{6}	1.07
Size	1	0.48x10^{6}	0.03
Herbicide	1	16.84x10^{6}	1.24 †
Time(days)	1	0.01x10^{6}	0.01
Plant tissue	3	0.11x10^{6}	0.01
S x H	1	28.51x10^{6}	1.60
S x T	1	9.76x10^{6}	0.55
S x P	3	5.44x10^{6}	1.59
H x T	1	16.54x10^{6}	0.93
H x P	3	12.11x10^{6}	3.53 *
T x P	3	5.25x10^{6}	1.53
S x H x T	1	17.75x10^{6}	5.18 *
S x H x P	3	2.52x10^{6}	0.75
H x T x P	3	0.87x10^{6}	0.25
S x T x P	3	1.82x10^{6}	0.53
S x H x T x P	3	4.98x10^{6}	1.45
Error	102	3.43x10^{6}	

* Significant at 5% level
† Tested against a composite error (HT + SHT)

Table A16. Analysis of variance of values for ^{14}C-herbicide recovered from root sections and the lower stem of different sized shoot-root systems treatment of the shoot (days pooled). Expt. 3.3.2.3. Values were adjusted by covariance using the total recovered radioactivity as the concomitant variable.

Source	D.F.	Mean Square	F
Replicates	7	5.00×10^{6}	1.02
Size	1	3.64×10^{6}	0.12
Herbicide	1	2.57×10^{6}	0.08
Tissue	3	0.11×10^{6}	0.02
S x H	1	30.74×10^{6}	6.68 *
S x T	3	5.44×10^{6}	1.18
H x T	3	12.11×10^{6}	2.63
S x H x T	3	2.52×10^{6}	0.55
Error	104	4.60×10^{6}	

* Significant at 5% level

Table A17. Analysis of variance of the ^{14}C-herbicide retained by lanolin. Expt. 3.3.3

Source	D.F.	Mean Square	F
Herbicide	1	140.14×10^{6}	26.88 **
Time(days)	2	0.73×10^{6}	0.14
H x T	2	15.45×10^{6}	2.96
Error	22 ‡	5.20×10^{6}	

** Significant at 1% level

‡ 2 d.f. lost from the error d.f. due to missing values